ABSTRACT

Title of Document: THE ECOLOGY OF EARLY CRETACEOUS ANGIOSPERMS: INSIGHTS FROM THE FOSSIL RECORD.

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The Early Cretaceous diversification of flowering plants was not preceded by a mass extinction event. This suggests that biotic factors intrinsic to flowering plants played an important role promoting diversification, but the rarity of fossils of early flowering plants makes identifying the important features difficult. Here, I present the results of my specimen-based analysis of plant megafossil collections from Lower Cretaceous deposits of the United States. First, I describe previously unrecognized eudicot leaf fossils from a historically important Aptian (Lower Cretaceous) plant fossil site in the Potomac Group, and I provide a set of characters for recognizing the fossil leaves of these plants. Then, I present a morphotype catalog for the fossil plants from and Aptian-early Albian (Lower Cretaceous) site in the Potomac Group. This collection includes one angiosperm morphotype. Next I describe the angiosperm morphotype identified in the previous chapter. I show that it is widely distributed

among coeval collections of the Potomac Group and some specimens were previously described as ferns. The preservation of attached stems leaves and root provides direct evidence of weedy, fast-growing, herbaceous angiosperms in the Aptian-early Albian. In the following chapter, I use megafossil data from the literature and museum collections to test the hypothesis that the diversification of flowering plants is associated with an increase in alpha diversity during the Early Cretaceous. Despite the evidence for a high diversification rate among early flowering plants, I found no relationship between collection age and collection richness, but I found strong evidence that angiosperms were consistently rare during the Aptan-middle Albian, and that locally abundant angiosperms became common during the late Albian, long after the initial diversification. Finally, I use new plant megafossil collections that I made from the Cloverly and Sykes Mountain Formations in Wyoming, USA, for a more high-resolution study of early angiosperm diversity, distribution, and abundance. I show that the Cloverly Formation records the appeareance of flowering plants in North America, and that by the Albian angiosperms were widely distributed among available habitats. I test the hypothesis that variation in community composition (beta diversity) increased with the appearance of angiosperms. I did not find strong support for the hypothesis that angiosperms increased beta diversity; however, rarefaction analysis shows that the rate of morphotype discovery in both the pre-angiosperm and the angiosperm interval is high, which means that additional sampling may reveal a difference in beta diversity between the two intervals. Together my findings indicate that flowering plants diversified during the Early Cretaceous not because they had features that allowed them to displace other plant

groups, but because they were uniquely able to maintain high diversification rates in the face of rarity and dispersed populations.

THE ECOLOGY OF EARLY CRETACEOUS ANGIOSPERMS: INSIGHTS FROM THE FOSSIL RECORD.

By

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Chapter 1: A new Early Cretaceous angiosperm from the Potomac Group and its implications for the evolution of eudicot leaf architecture

Abstract

• *Premise of the study:* Eudicots diverged early in the evolution of flowering plants and now comprise more than 70% of angiosperm species. In spite of the importance of eudicots, our understanding of the early evolution of this clade is limited by a poor fossil record and uncertainty about the order of early phylogenetic branching. The study of Lower Cretaceous fossils can reveal much about the evolution, morphology, and ecology of the eudicots.

• *Methods:* Fossils described here were collected from Aptian sediments of the Potomac Group exposed at the Dutch Gap locality in Virginia, USA. Specimens were prepared by degaging, then described and compared with leaves of relevant extant and fossil plants. We conducted a phylogenetic analysis of morphological characters using parsimony while constraining the tree search with the topology found through molecular phylogenetic analyses.

• *Key results:* The new species is closely related to ranunculalean eudicots and has leaf architecture remarkably similar to some living Fumarioideae (Papaveraceae).

• *Conclusions:* These are the oldest eudicot megafossils from North America, and they show complex leaf architecture reflecting developmental pathways unique to extant eudicots. The morphology and small size of the fossils suggest that they were herbaceous plants, as is seen in other putative early eudicots. The absence of co-

occurring tricolpate pollen at Dutch Gap either (1) reflects low preservation probability for pollen of entomophilous herbs or (2) indicates that some leaf features of extant eudicots appeared before the origin of tricolpate pollen.

Introduction

The current model of angiosperm phylogeny recognizes a grade of basal lineages (*Amborella*, Nymphaeales, Austrobaileyales), and five monophyletic groups: Chloranthales, magnoliids, monocots, *Ceratophyllum*, and the eudicots (Bremer, 2009). The eudicots comprise more than 70% of all extant angiosperm species. The oldest eudicot fossils are tricolpate pollen grains from the latest Barremian (Early Cretaceous) of equatorial Gondwana (Hughes et al., 1991; Doyle, 1992), providing a minimum age of ~126 Ma for the split between eudicots and their sister clade. These eudicot pollen grains are less than 8 million years younger than the oldest fossil angiosperm pollen, which comes from Hauterivian deposits in England (Hughes et al., 1991; Hopson et al., 2008), Israel (Brenner and Bickhoff, 1992; Brenner, 1996; Segev, 2009), and possibly Italy (Trevisan, 1988).

Remarkably, the early history of eudicots is poorly understood. The oldest fossils that have synapomorphies of clades nested within eudicots come from mid-Albian deposits (Upchurch, 1984a; b; Crane et al., 1993; Doyle and Endress, 2010). These fossils document the presence of crown-group eudicots, but are more than 16 million years younger than the oldest tricolpate pollen grains. A few putative eudicot megafossils have been described from the intervening Aptian and early Albian (Table 1 and citations therein), and others may exist in the published literature (e.g. Sun and Dilcher, 2002), but a phylogenetic position nested within crown-group eudicots has

not been demonstrated for any of these. Given the available evidence, it is possible that some of these plants represent stem-lineages along the branch leading to crown-group eudicots (eudicots s.l., as opposed to crown-group eudicots, hereafter eudicots s.s.), or that they are not eudicots at all (Doyle, 2012).

Here we describe a new genus and species of angiosperm with remarkable similarity to extant members of the subfamily Fumarioideae (Papaveraceae, Ranunculales). The leaf fossils were collected from the Aptian Dutch Gap locality, near Richmond, Virginia USA, which is among the oldest angiosperm-bearing fossil sites in North America (Doyle and Hickey, 1976; Doyle and Robbins, 1977). We compare these fossils with the leaves of living angiosperms, ferns, and other putative eudicots from the Aptian-mid Albian. We infer the phylogenetic position of the new fossils from parsimony analysis, and their paleoecology and paleoenvironment from functional morphology of leaves, sedimentary context, and from co-occurring fossils.

Methods

Geologic and Depositional Setting

The fossils are preserved as compressions in a silty clay bed near the base of the Potomac Group exposure at Dutch Gap in Henrico County, Virginia, USA (Fig. 1). The Potomac Group beds at Dutch Gap are exposed along the south bank of the James River. The fossils we examined were collected at three different times. LJH and James A. Doyle collected USNM specimen 559298 (Figs. 3, 4) in 1971 (JAD/LJH locality 71-111). In 1990 David W. Taylor collected YPM specimen 6815 (not figured). In 1991 LJH collected YPM specimen 60058 (Fig. 5) (LJH locality 91-11). A party led by NAJ returned to the site in 2013, but it had been covered with

riprap to prevent erosion of the bank so the original collecting site was no longer accessible.

The Potomac Group comprises, in stratigraphic order, the Patuxent Formation, the Arundel Clay, and the Patapsco Formation. The upper and lower units are often undifferentiated lithologically. The pollen zones of Brenner (1963) and Doyle and Robbins (1977) provide biostratigraphic control on the age of lithologically undifferentiated Potomac Group deposits. The beds at Dutch Gap belong to the lower part of pollen Zone I, which was once thought to be as old as Barremian (Brenner 1963; Doyle and Robbins 1977) but is now considered to be Aptian (Fig. 2) because of the presence of *Pennipollis* (formerly *Retimonocolpites*) *peroreticulatus* (Brenner 1963) Friis, Pedersen et Crane 2000 (Upchurch and Doyle, 1981; Doyle, 1992; Hochuli et al., 2006).

Fossil Preparation

The blocks of fossiliferous sediment are curated in the Department of Paleobiology, National Museum of Natural History, Smithsonian Institution (NMNH), and in the Division of Paleobotany at the Peabody Museum of Natural History, Yale University (YPM). Since their collection they have dried out and become amenable to splitting along bedding planes and preparation by degaging. The fossils were photographed using a Canon EOS digital camera with a 100mm EF macro lens. The images were processed with Adobe Photoshop (San Jose, California, USA). Venation of the fossils was traced by hand from prints of digital photos and traced with a mouse on a digital image in Adobe Photoshop. The two tracings for each of two fossils were then compared and reconciled using photographs of the

fossils taken under different lighting conditions. We used the image stacking function in Adobe Photoshop to generate photo illustrations in which the entire fossil is in focus (Fig. 3). Leaves of extant species on herbarium sheets housed at the United States National Herbarium at the National Museum of Natural History (US) were photographed using a Macro Twin Lite MT-24EX Canon flash arranged below the herbarium sheets to pass light through the specimens. Vein density was measured from images using the program ImageJ (Rasband, 1997-2012).

Phylogenetic Analysis

We used the molecular scaffold approach described by Springer et al. (2001) to determine the most parsimonious position of the fossils in the angiosperm phylogeny (Springer et al., 2001). The tree search was constrained by the relationships reported by Bremer, (2009), Barniske et al. (2012), and Hoot et al. (1997) for 41 genera of ANA-grade angiosperms, magnoliids, Chloranthales, Monocotoledonae excl. Commelinidae (hereafter “basal monocots”), and Eudicotyledonae excl. Pentapetalae (hereafter “basal eudicots”). Only the position of the new fossil described below was free to vary.

We scored 14 leaf characters for 42 genera (Appendices 1&2). If multiple character states are present for a single character within a genus or species, all were recorded in the matrix. If character states could not be scored for a genus because it lacks the character (i.e. the character "leaflet venation" cannot be scored in plants with simple leaves), we followed Hawkins et al. (1997) and Strong and Lipscomb (1999) in assigning the value “?” for those fields. We also included some extinct genera of known phylogenetic position in the analysis as terminal taxa in order to

capture the range of the morphological variation in lineages that have low extant diversity. *Sapindopsis* is included as a stem-genus along the branch leading to modern *Platanus* (Crane et al. 1993); and *Exnelumbites* is included as a stem-genus along the branch leading to modern *Nelumbo* (Estrada-Ruiz et al., 2011). All characters were unweighted and unpolarized and we specified *Amborella* as the outgroup. Multistate characters were unordered. We performed parsimony analyses using PAUP*v4.0b (Swofford, 2002).

We did not include taxa from more derived groups that radiated in the Late Cretaceous and Cenozoic because many taxa in these groups have characters and character states that are highly divergent from those present in the fossils, making it difficult or impossible to assess homology. Uncertainty about the homology of characters and characters states between the fossils and derived eudicots would force us to score characters of the latter as "?" in the matrix. This would tend to obscure the phylogenetic position of the fossil.

Character definitions were based on those outlined in the Manual of Leaf Architecture (Ellis et al., 2009), with three exceptions. First, leaf dissection characters (numbers 6 & 7) were coded using ontogenetic types observed in Papaveraceae (Gleissberg and Kadereit, 1999). The ontogenetic types correlate with gradients in leaflet size and depth of laminar dissection that can be observed in mature leaves (Gleissberg and Kadereit, 1999). Compound leaves of genera not in Papaveraceae were scored using the same system after consulting work on the development of leaf dissection in those taxa (Turlier, 1979; Sugiyama and Hara, 1988; Pabón-Mora and González, 2012), and reviewing ontogenetic series of leaves in photographs and

herbarium specimens. Second, the states for character 10 (tooth morphology) were simplified to glandular, simple, or spinose because it is often difficult to distinguish among the different tooth types in fossils, as outlined by Ellis et al. (2009). This means that teeth scored as "glandular" may or may not be anatomically similar. Third, we included "reticulodromous" as a character state for primary vein framework (characters 13 & 14) even though Ellis et al. (2009) considered it a character state for secondary vein framework. We used "reticulodromous" for leaves in which the primary and secondary veins were indistinguishable in their course and gauge.

Finally, we used Mesquite (Maddison and Maddison, 2011) to determine the length of most parsimonious trees under different phylogenetic scenarios. We compared the length of trees in which *Euptelea* was sister to core Ranunculales, sister to Papaveraceae, and sister to both, as well as trees with *Ceratophyllum* sister to eudicots, to monocots, and to both.

Results

Systematics

Class–Magnoliopsida Cronquist, Takhtajan, and Zimmermann, 1966.

Order–cf. Ranunculales Jussieu ex Berchtold & J. Presl, 1820.

Family–cf. Papaveraceae Jussieu 1789.

Subfamily–cf. Fumarioideae Eaton, 1836.

Genus– *Potomacapnos* gen. nov.

Species– *Potomacapnos apeleutheron* gen. et sp. nov.

Combined generic and specific diagnosis–Leaves composed of small, obovate, toothed, and asymmetrically lobed leaflets with an indistinct lamina-petiolule

transition. Marginal indentations grade continuously from teeth to lobes. Teeth are glandular, with the principal vein derived from a primary or secondary vein that enters the tooth medially. Accessory veins enter the teeth laterally and are part of an intramarginal secondary vein. Primary vein framework is reticulodromous. Primary and secondary veins produce low angle dichotomies and anastomose rarely. The primary and secondary veins fuse with the intramarginal vein, which thickens near the apices of the teeth. This thickening may be the result of specialized secretory tissues, the buildup of secretory products, or increased production of sclerenchymatous tissue. Tertiary veins are rare, forming a faint reticulum that connects with the major (primary and secondary) veins primarily in the widest, distal portions of the lamina.

Holotype here designated–USNM specimen 559298 is housed in the type collection in the Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington D.C. (Figs. 3-5)

Paratypes–YPM specimens 6815 (Fig. 6) and 60058 are housed in the Division of Paleobotany at the Peabody Museum of Natural History, Yale University, New Haven CT.

Etymology– Potomacapnos comes from the Potomac Group, the geologic unit from which the fossils were collected, and kapnos, the Greek word used for smoke. Extant genera in the Fumarioideae are commonly called fumitories or smoke worts. The type genus is *Fumaria*, derived from the latin fumus (smoke), whereas several other genera (e.g. *Capnoides*, *Lamprocapnos*, *Trigonocapnos*) use the Greek word for smoke. The use of kapnos in *Potomacapnos* is meant to emphasize the morphological

similarity between the fossil and modern fumitories. The specific epithet *apeleutheron* is the plural genitive case of the Greek word apeleutheros, meaning freedman. This name honors the freedmen who dug the Dutch Gap Canal in Virginia during the United States Civil War in 1864, exposing the sediments from which this fossil was collected. Men of the Roanoke Island Freedmen's Colony in North Carolina were forcibly taken from their work at Fort Reno and from the colony by press gangs to dig the Dutch Gap Canal in August, 1864 under the orders of Union Generals Palmer and Butler. Some of the details of this ordeal are given in a letter written by freedmen N. Baxter and S. Owens on behalf of the freedmen who had not been paid for their labor (Baxter and Owens, 1864 *in* Berlin et al. 1993).

Collecting locality–Dutch Gap, Virginia, USA. N37.375° W-79.359° WGS84, LJH and JAD 71-117 and LJH 91-11.

Stratigraphic position and Age– Lower part of Pollen Zone I, Potomac Group; Aptian, Early Cretaceous.

Description–Leaflets obovate and 12-18 mm long with up to five lobes arranged asymmetrically (Fig. 3). There is no indication of a node or axis where the leaflets attach to one another in USNM specimen 559298, and the transition between lamina and petiolule is indistinct, indicating that the fossil is a fragment of compound leaf (Fig. 3). The left leaflet is rotated in the holotype, and on the same specimen, the large principal lobe on the right leaflet bears two asymmetrical lateral lobes (Fig. 3). The smaller principal lobe bears only one lateral lobe, which is also located exmedially. All lobes terminate in glandular teeth with accessory veins that are continuous with the intramarginal vein. In larger lobes the intramarginal accessory

veins are conspicuously thickened and thin gradually away from the apex (Fig. 4). As the lamina widens toward the apex the number of major veins increases via low-angle dichotomies. All major veins intersect the strong intramarginal vein that extends along the distal margin of the leaflets. Minor (tertiary) veins are rare, but can be seen in the wider, distal portions of the lamina where they reticulate with each other and with the major veins (Fig. 6). Areolation is highly irregular and freely ending veinlets have not been observed. Vein density in the major lobe is 2.55mm/mm^2.

Phylogenetic Analysis

The tree search yielded three most parsimonious trees of 77 steps, with *Potomacapnos apeleutheron* in one of the following positions: (i) sister to a clade including *Fumaria* and *Corydalis*, (ii) sister to *Corydalis*, or (iii) sister to *Fumaria*. The strict consensus tree is shown in Fig. 7. Trees in which *Potomacapnos* is sister to *Hypecoum* or sister to the clade [*Hypecoum*, [*Corydalis*, *Fumaria*]], are one step longer (78); no trees were found that are two steps longer than the shortest tree (79). Some alternative positions of *Euptelea* and *Ceratophyllum* in the constraint tree lengthened the overall tree by one step, but did not affect the most parsimonious position of *Potomacapnos*. Most of the character states observed in the fossils also occur outside of Fumarioideae; however, the combination of characters seen in *Potomacapnos* can only be found in extant Fumarioideae.

Discussion

Comparisons with Extant and Fossil Plants

The variability of leaf form among extant eudicots makes identifying leaf architectural synapomorphies challenging, but the identification of such characters will allow paleobotanists to identify eudicot megafossils and better understand the radiation of flowering plants from the fossil record. Geeta et al. (2012) found moderate support for complex/lobed leaves as the ancestral condition for eudicots in their analysis of 409 extant species, but the trait "complex leaves" is clearly independently derived many times. Complex leaves occur outside of the eudicot clade (e.g., monocots, the genus *Illigera* in Laurales); and even within eudicots there are many lineages with complex leaves that originated independently from simple-leaved ancestors. Gene expression studies have shown that complex leaf development across different eudicots and monocots is governed by various genetic pathways that only partially overlap (Bharathan and Sinha, 2001; Groot et al., 2005; Champagne et al., 2007; Blein et al., 2008; Efroni et al., 2010; Ikeuchi et al., 2013).

Gleissberg and Kadereit (1999) used comparative ontogenetic data to clarify and classify the various types of complex leaf development in Papaveraceae. They expanded the classical categories of leaf dissection of Trécul (1853), Prantl (1883), and Hagemann (1970) (acropetal, basipetal, divergent, and polyternate) to include six modes of leaf dissection grouped into three classes based on directionality of leaf segmentation during onotogeny. These three classes are (1) Polyternate/Acropetal/Basipetal-pedate (PABpe) dissection, (2) Basipetal pinnate (Bpi) dissection, and (3) undissected or simple. The presence of each developmental

pattern in a given species can be determined by examining ontogenetic series, and sometimes can be determined from adult morphology alone (Ikeuchi et al., 2013). These three categories can also be applied to other "basal" eudicots with complex leaves (Sugiyama and Hara, 1988; Pabón-Mora and González, 2012). An additional category of leaf dissection, basipetal-palmate, appears to be represented in some Lardizabalaceae (Sugiyama and Hara, 1988).

We scored *Potomacapnos* as "(1) present" for PABpe leaf dissection because the asymmetric arrangement of lobes and teeth seen in *Potomacapnos* is also seen in extant species of Ranunculales with leaf architecture intermediate between polyternate and basipetal pedate and that undergo asymmetrical ternation on the basiscopic margin of lateral lobes or leaflets. In addition to PABpe leaf dissection, other characters that conservatively support the eudicot s.l. affinities of *Potomacapnos* include the presence of glandular teeth, an intramarginal vein that is thickened near the teeth, primary and secondary veins that intergrade in course and gauge, reticulodromous major venation, and absence of freely ending veinlets. This combination of characters is common in extant Fumarioideae (Figs. 8-10) and many of these characters also occur in other herbaceous Ranunculales.

Prior work on the ontogeny of leaves outside of eudicots shows they generally do not fit the classification scheme of Gleissberg and Kadereit (Kaplan, 1973; Turlier, 1979; Periasamy and Muruganathan, 1986; Gunawardena and Dengler, 2006). Trifoliate and palmate-pentafoliate leaves occur in *Cabomba*, *Illigera*, and some reticulate-veined monocots (e.g. *Arisaema* spp.). Pinnately compound, palmately compound, and distinctive compound leaves with adult morphology similar to

basipetal-pedate leaves in Ranunculales all occur in monocots (e.g. *Arisaema tortuosum*, *Amorphophallus* spp.). Developmental studies of leaves in *Cabomba* (Turlier, 1979) and monocots (Kaplan, 1973; Periasamy and Muruganathan, 1986; Gunawardena and Dengler, 2007; Jouannic et al., 2007) show that the segmentation pattern in these leaves is different from those patterns found in Ranunculales. We infer that compound leaves in these groups are probably not homologous with the compound leaves in eudicots, implying that the genes for compound leaf development were recruited independently. Unfortunately, with the exception of some monocots (Jouannic et al., 2007), the genetic basis of compound leaf development in non-eudicot angiosperms is not well understood. Our analysis suggests that although compound leaves do occur rarely in the other major clades of angiosperms, eudicots may have a unique potential for developing many different kinds of complex leaves, and that polyternate, intermediate polyternate-basipetal pedate, and compound basipetal pinnate leaves are unique to eudicots among extant angiosperms.

We interpret *Potomacapnos* as a eudicot s.l., but recognize that in some characters *Potomacapnos* resembles some ferns. Hierarchical reticulate (complex reticulate) venation, absence of freely ending veinlets in combination with reticulate venation, intramaginal (commissural) veins, and asymmetrically lobed pinnae can all be found in some ferns, but these are rarely found in combination. Some species of *Adiantum* combine marginal teeth and asymmetrically lobed pinnae (Fig. 11), but their teeth are never glandular, and venation generally lacks reticulation. Some species of *Ceratopteris* combine simple reticulate venation and asymmetrically lobed pinnae (Fig. 12), but in these species areole shape is regular and areole size decreases

smoothly from the midvein toward the margin. In addition, all *Ceratopteris* lack an intramarginal vein, glandular teeth, and a reticulum of tertiary veins. Some members of Tectariaceae and bulbitoid Dryopteridaceae (Moran et al., 2010) have angiosperm-like leaves because they have hierarchical reticulate venation, asymmetrically lobed pinnae, marginal teeth, and freely ending veinlets (Figs. 13, 14). However, areolation in these ferns is distinctively and regularly polygonal, and secondary or tertiary veins are stereotypically deflected at junctions with finer veins. These similarities between some fern leaves and typical angiosperm leaves are clearly convergent when examined in detail, and the common ancestor of ferns and angiosperms appears to have lacked stem-leaf organography (Tomescu, 2009).

Studies of leaf fossils in the Potomac Group in the 1970s showed patterns of increasing diversity, abundance, and distribution among depositional environments, as well as increasing average structural rigidity (as indicated by leaf rank) from the Aptian through the Cenomanian (Doyle and Hickey, 1976; Hickey and Doyle, 1977). The angiosperm leaves of the lower part of pollen Zone I are rare, small, and simple, with mostly pinnate primary venation, although *Acaciaephyllum* has parallelodromous/acrodromous major veins and *Proteaephyllum reniforme* has flabellate primary venation (Fontaine, 1889; Berry, 1911; Doyle and Hickey, 1976). The presence of *Potomacapnos* at Dutch Gap shows that angiosperm leaf morphology was more diverse than previously known in lower Pollen Zone I.

Some of the fossils from lower Pollen Zone I of the Potomac Group have been identified as monocots and ANA-grade angiosperms (Fontaine, 1889; Upchurch, 1984a; b; Doyle et al., 2008). Dispersed cuticles also indicate the presence of ANA-

grade angiosperms in lower Pollen Zone I (Upchurch, 1984b). Tricolpate pollen, indicative of eudicots, has not been reported from the deposits at Dutch Gap; however, a few isolated grains were reported from offshore Zone I correlative deposits (Doyle, 1992). If *Potomacapnos* is indeed a eudicot s.s. as suggested by our phylogenetic analysis, then the absence of tricolpate pollen at Dutch Gap is surprising. We offer two possible explanations. Tricolpate pollen could be absent because *Potomocapnos* was small, rare, and produced little pollen -- features associated with entomophylly. Alternately, *Potomocapnos* may not have produced tricolpate pollen because it was a eudicot stem lineage above the origin of eudicot-type leaves but below the origin of tricolpate pollen. Additional fossils comprised of multiple organs are required to resolve this issue.

Ecological Implications

From an ecological perspective the diversity of leaf form is governed by complex, interrelated trade-offs between light capture, the economics of gas exchange, water supply, structural rigidity, and defense against herbivores and pathogens (Givnish, 1987; Wright et al., 2004; Sack and Holbrook, 2006; Brodribb et al., 2007; Nicotra et al., 2011; Osnas et al., 2013). Leaf architectural characters are thus not easy to interpret in the context of ecology, however certain patterns emerge across the diversity of angiosperm leaves that when taken together can be useful in interpreting the autecology of fossil plants (Wing and Boucher, 1998). Variably compound or deeply lobed leaves are common in ruderal herbs and shrubs (Givnish 1987; Wing and Boucher 1998). Small leaves are typical of herbs, and most plants in seasonal or dry climates (Peppe et al., 2011). Large teeth and relatively disorganized,

low density venation (e.g. low rank leaves) are common features of shade-tolerant dicots (Hickey and Doyle, 1977; Feild et al., 2004, 2009).

Potomacapnos, like extant fumarioids, has compound leaves with deeply lobed leaflets, large glandular teeth, and poorly organized (low-rank) venation. This similarity could reflect retention of ancestral features in living herbaceous poppies rather than shared derived features of crown group Fumarioideae. If this is the case, we suggest that retention of these features is driven by similarity in ecological function. Extant fumarioids are small-seeded annual or perennial rhizomatous or climbing herbs (Pérez-Gutiérrez et al., 2012) with vein densities as low as 2.0mm/mm^2 (*Fumaria sp.* NCLC-H 6702), and are known to colonize disturbed patches, such as logs and pits in forested ecosystems (Thompson, 1980; Ehlers and Olesen, 2004). We infer that *Potomacapnos* had a similar ruderal life history strategy.

Analysis of the sedimentology at Dutch Gap also supports similar climatic preferences for *Potomacapnos* and extant fumarioids, most of which are native to areas with seasonal temperate or Mediterranean climates (Hutchinson, 1921). Our material of *Potomacapnos* was collected from a medium gray silty clay bed with planar fabric, but no evident lamination except near its contact with the underlying sand bed (Upchurch and Doyle, 1981). Larger clasts in the silty clay matrix are primarily organic debris (e.g. charcoal fragments, megaspores) or mica flakes. There is no evidence of flaser bedding, ripples, or strong bioturbation that would indicate tidal influence (Upchurch and Doyle, 1981). The most common megafossils are foliage of the bennettitalean plant *Dioonites buchianus* and occasional compressions of bracts that subtend strobili, which are comparable to the bennettitalean

Williamsonia. These two organs likely represent the same plant. Foliage of ferns (Schizaeales) and conifers (Cheirolepidiaceae and taxodiaceous Cupressaceae) is common. Mesofossils from Dutch Gap have revealed additional diversity, including the seeds and pollen organs of enigmatic gymnosperms (Pedersen et al., 1993). This type of Bennettitalean and Conifer dominated flora with several species of ferns is typical of Early Cretaceous subtropical floodplain assemblages (Vakhrameev, 1987). During the 2013 return to Dutch Gap, NAJ examined small exposures of the lower part of Pollen Zone I a few meters above the level from which *Potomacapnos* was collected. Here, blocky clay beds alternate with sandy siltstone beds and matrix-supported cobble-conglomerate beds. *Dioonites* fragments dominate in the clay beds and sandy siltstones, but fern fragments and conifer shoots assignable to Cheirolepidiaceae and taxodiaceous Cupressaceae were also found. Together, the available sedimentological information suggests alternating periods of low-energy deposition and very high energy deposition, typical of fluvial systems in a seasonal climate, or possibly storm deposits.

The description of *Potomacapnos apeleutheron* contributes to an emerging picture of early (Hauterivian-Aptian) flowering plants as locally rare, herbaceous plants that were nevertheless geographically widespread and morphologically diverse. The evidence for the herbaceous habit comes from the characters described above in *Potomacapnos*, as well as other characters observed in other early angiosperm fossils (Taylor and Hickey, 1990; Sun et al., 1998; Leng and Friis, 2003; Doyle et al., 2008; Mohr et al., 2008) and from the virtual absence of Hauterivian-Aptian angiosperm wood fossils (Stopes, 1913; Nishida, 1962; Suzuki and Nishida, 1974 but see Hughes,

1976; Oh et al., 2011), despite the abundance of fossil gymnosperm wood (Philippe et al., 2008; Peralta-Medina and Falcon-Lang, 2012). The fossil evidence for herbaceous habit in early angiosperms, and in particular early eudicots and monocots, superficially conflicts with phylogenetic studies of living plants in which the common ancestor of both eudicots and crown-group angiosperms is reconstructed as woody (Kim et al., 2004). This conflict is resolved if a vascular cambium was present in the common ancestors of eudicots but its activity was limited as in many modern herbs and small shrubs (Stebbins, 1965a; Groover, 2005).

Conclusions

Potomacapnos apeleutheron has a combination of leaf architectural synapomorphies and plesiomorphies that support a relationship with crown-group Ranunculales, but based on the age of the fossils and their fragmentary nature we cannot exclude a phylogenetic position as a ranunculalean- or eudicot-stem lineage. Rather than indicating membership in crown-group Papaveraceae, the strong morphological similarity of *Potomacapnos* to many extant Fumarioideae may reflect ecological similarity and the retention of ancestral features in some modern herbaceous poppies. The superficial similarity of *Potomacapnos* to the foliage of some ferns is a result of evolutionary convergence between analogous megaphylls.

The description of *Potomacapnos apeleutheron* adds to the diversity of angiosperm leaf types known from the Potomac Group and confirms the presence of herbaceous angiosperms with eudicot-type vegetative features at an early stage in angiosperm evolution. Rarity and the herbaceous habit were probably characteristic of eudicots during the earliest phase of their diversification.

Tables and Figures

Table I. Putative Early Eudicot Megafossils. Age and important features of Aptian to mid-Albian megafossils (and one mesofossil: *T. lusitanica*) that have been compared with or assigned to eudicots or Ranunculales. 1. Krassilov and Volynets, 2008; 2. Sun et al., 1998; 3. Sun et al., 2002; 4. Friis et al., 2003; 5. Doyle and Endress, 2010; 6. Puebla, 2009; 7. Sun et al., 2011; 8. Samylina, 1968; 9. Bravi et al., 2010; 10. Leng and Friis, 2003; 11. Leng and Friis, 2006; 12. von Balthazar et al., 2005; 131. Fontaine, 1889.

Species	Age	Characters used to infer eudicot affinity
Achaenocarpites capitellatus[1]	104-113Ma	Herbaceous habit, leaves three-fold to pedate, fruit achene
Archaefructus spp.[2,3,4,5]	123-127Ma	Herbaceous habit, Compound leaves
LC-Microphyll trifoliate[6]	113-120Ma	Trifoliate compound leaf, Glandular teeth
Leefructus mirus[7]	123-124Ma	Basally syncarpous gynoecium, Trilobed leaves, Herbaceous habit
Ranunculaecarpus quinquecarpellatus[8]	104-113Ma	Apocarpous fruit, Capsular fruit
Sagaria cilentana[9]	104-109Ma	Lobed leaves, Glandular teeth, Superior gynoecium, Capsular fruit, Cymose infructescence
Sinocarpus decussatus[10,11]	123-124Ma	Herbaceous habit, Glandular teeth, Compound inflorescence, Superior gynoecium, Basally syncarpous gynoecium
Teixeiraea lusitanica[12]	109-115Ma	Tricolpate pollen, Flowers microsporangiate, Numerous stamens, Helically arranged floral organs
Ternaricarpites floribundus[1]	104-113Ma	Herbaceous habit, pinnately lobed leaves, slightly zygomorphic perianth, fruit a follicetum
Vitiphyllum spp.[4,13]	109-115Ma	Trilobed leaves

Figure 1. Map of Lower Cretaceous Potomac Group outcrop in Virginia and Maryland, USA. The Dutch Gap locality is indicated by an arrow near the southern end of the outcrop area.

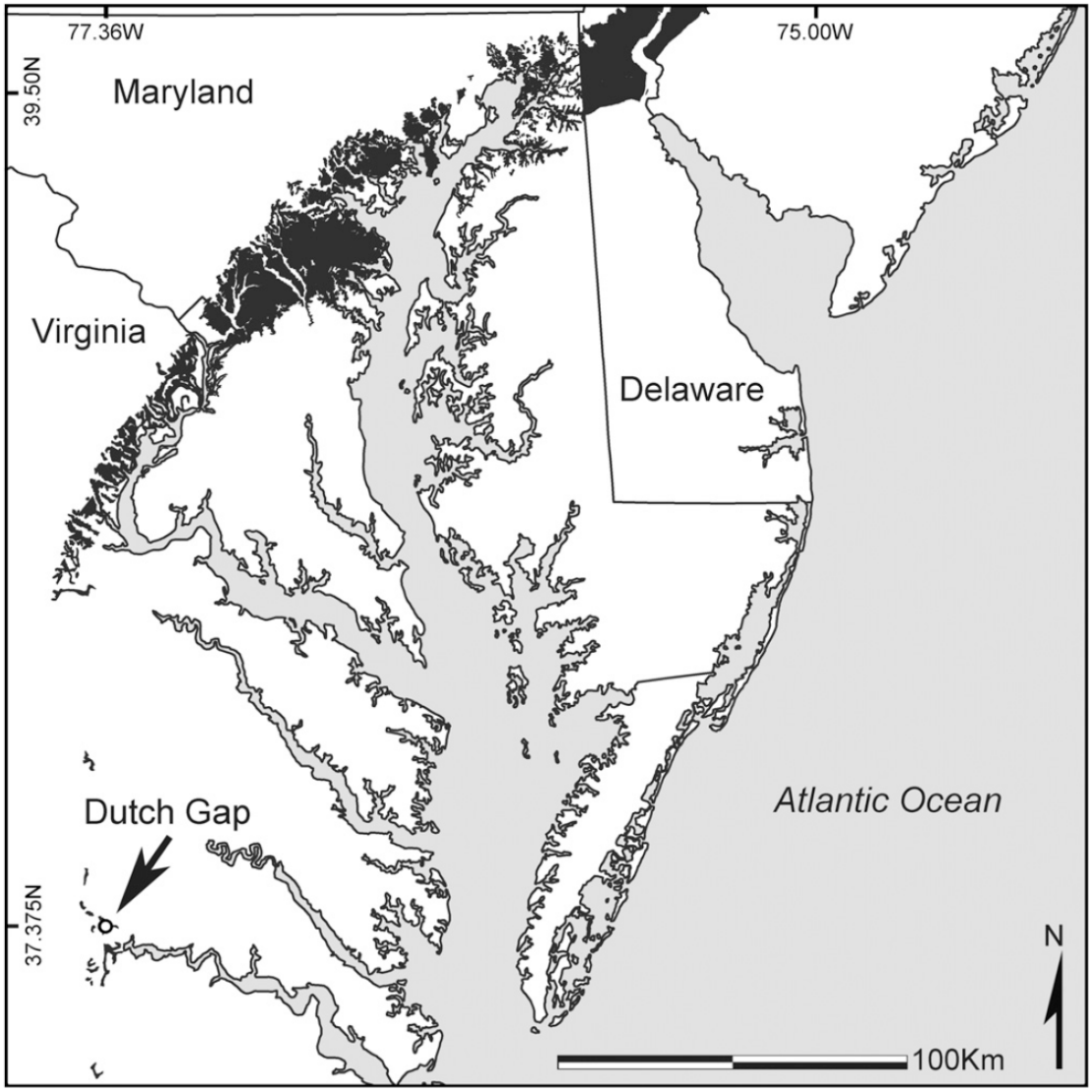
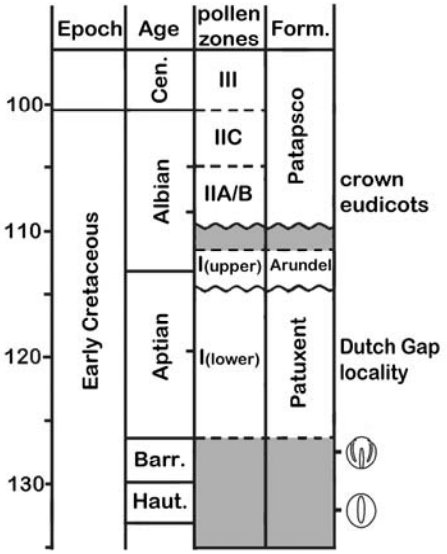


Figure 2. Age of the lower part of the Potomac Group (modified from Doyle, 1992; Hochuli et al., 2006; dates on the left are from Gradstein et al., 2012). The Dutch Gap locality is in the lower part of Zone I. Barr. = Barremian stage, Haut. = Hauterivian stage. Note the first occurrence globally of angiosperm pollen in deposits of Hauterivian age, and of tricolpate pollen in upper Barremian deposits. In the Potomac Group, angiosperm pollen first occurs in lower Zone I and tricolpate pollen is thought to first occur in upper Zone I. Unequivocally crown-group eudicots that have been described previously come from deposits as old as mid-Albian.



Figures 3–6. *Potomacapnos apeleutheron* gen. et sp. nov. **3,** USNM 559298 (Holotype) showing two lobed leaflets with reticulate venation, intramarginal vein, and glandular teeth. The right leaflet has two major lobes and three lateral lobes. The left leaflet has one major lobe and one minor lobe preserved. The left leaflet is folded under and twisted about its axis 180 °. It is 1–2 mm deeper in the matrix than the right leaflet. L: Major lobe, ll: lateral lobe. Scale bar = 5 mm. **4,** USNM 559298. Close-up of the right major lobe of the right leaflet from Figure 3 . Note the marginal tooth supplied by the thickened intramarginal vein at the white arrow. Also note the higher order reticulum indicated by the black arrow. Scale bar = 1 mm. **5,** YPM 6185. A single asymmetrical leaflet that is deeply lobed. Note that the right lobe is broader than the left lobe. Scale bar = 5 mm. **6,** Illustration of the venation of the fossil shown in (5) at the same scale. Note the deep division of the leaf fragment into two major lobes.

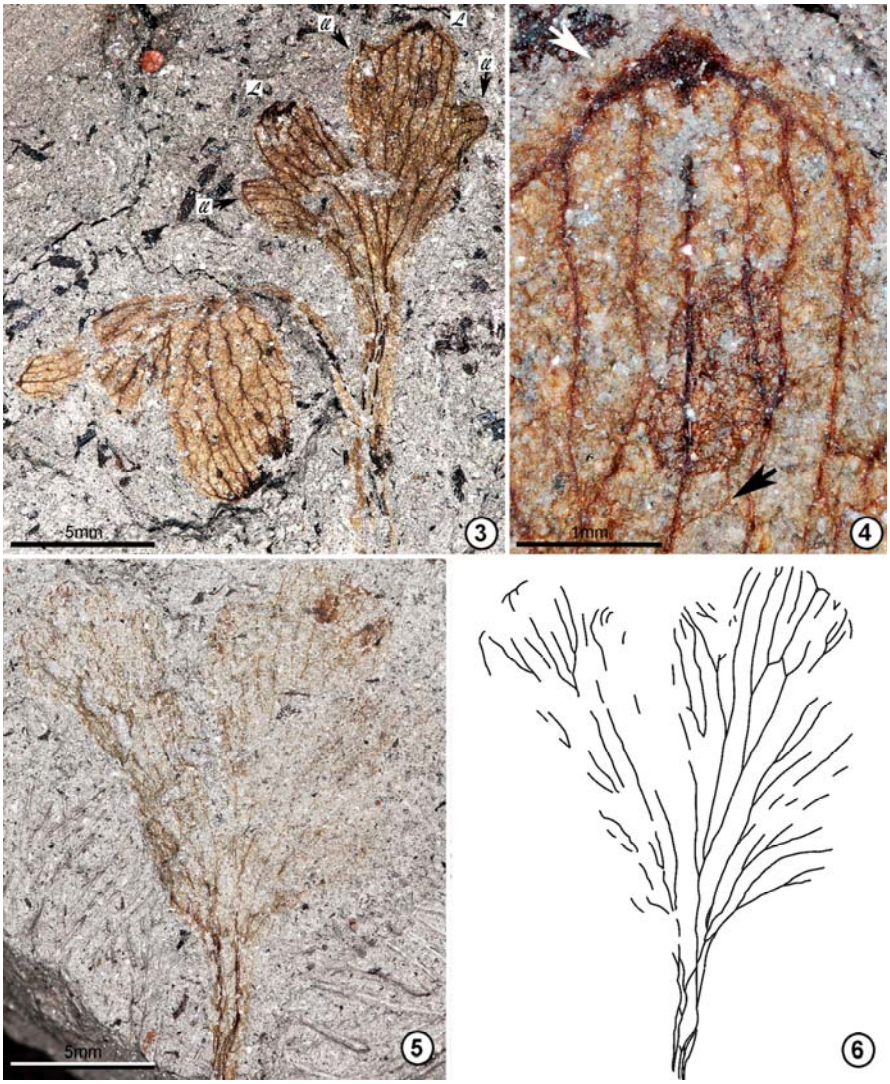
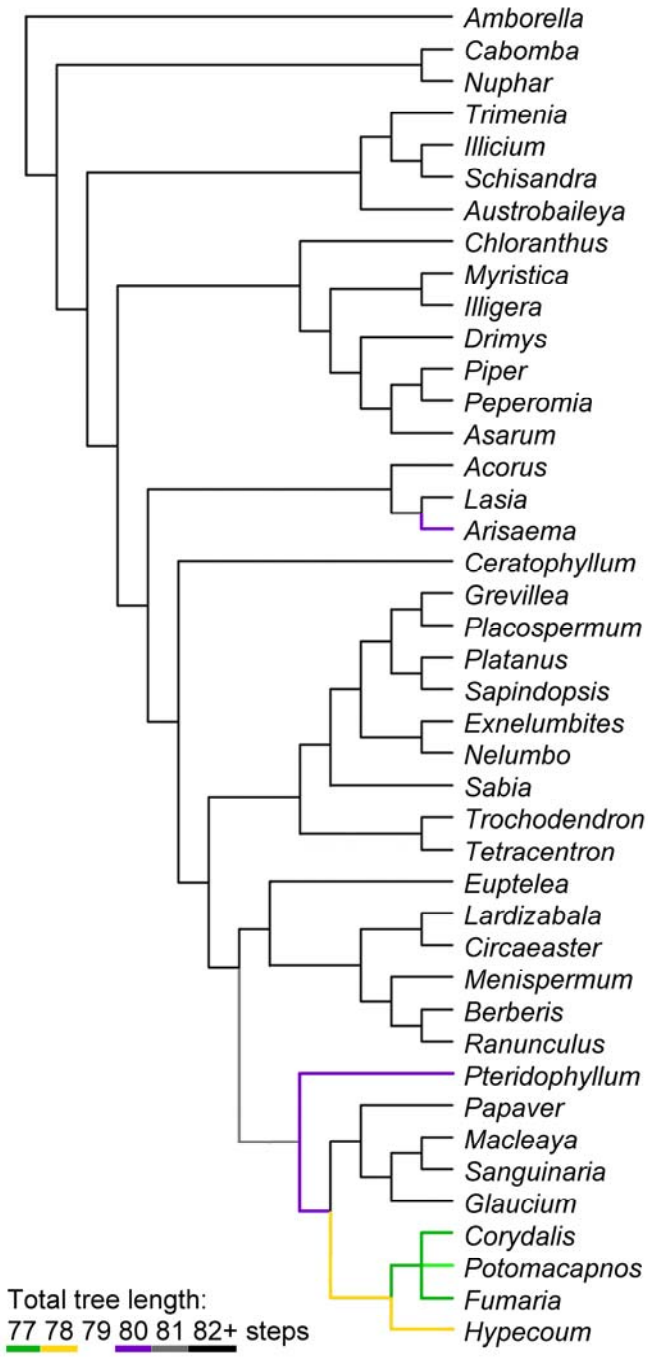
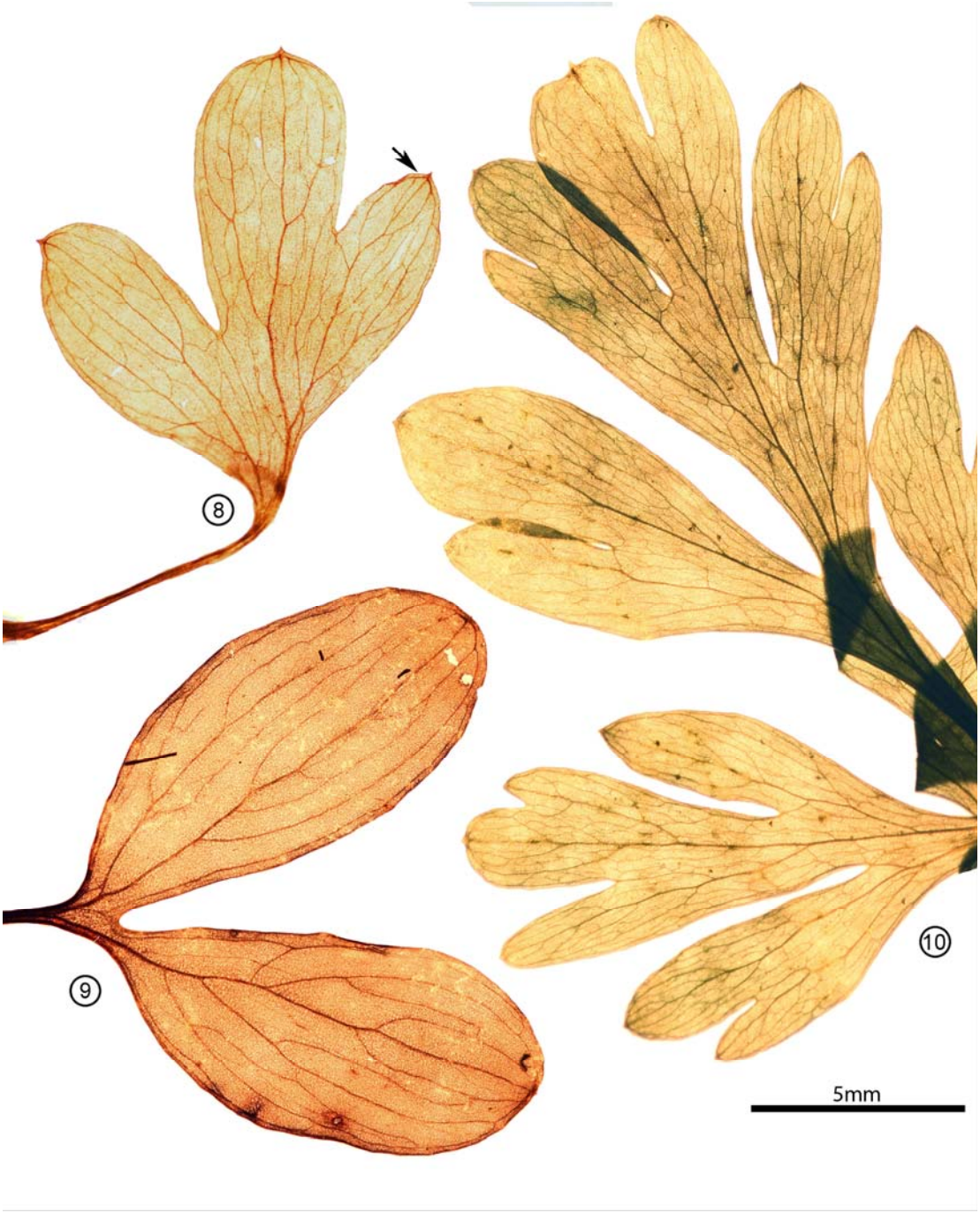


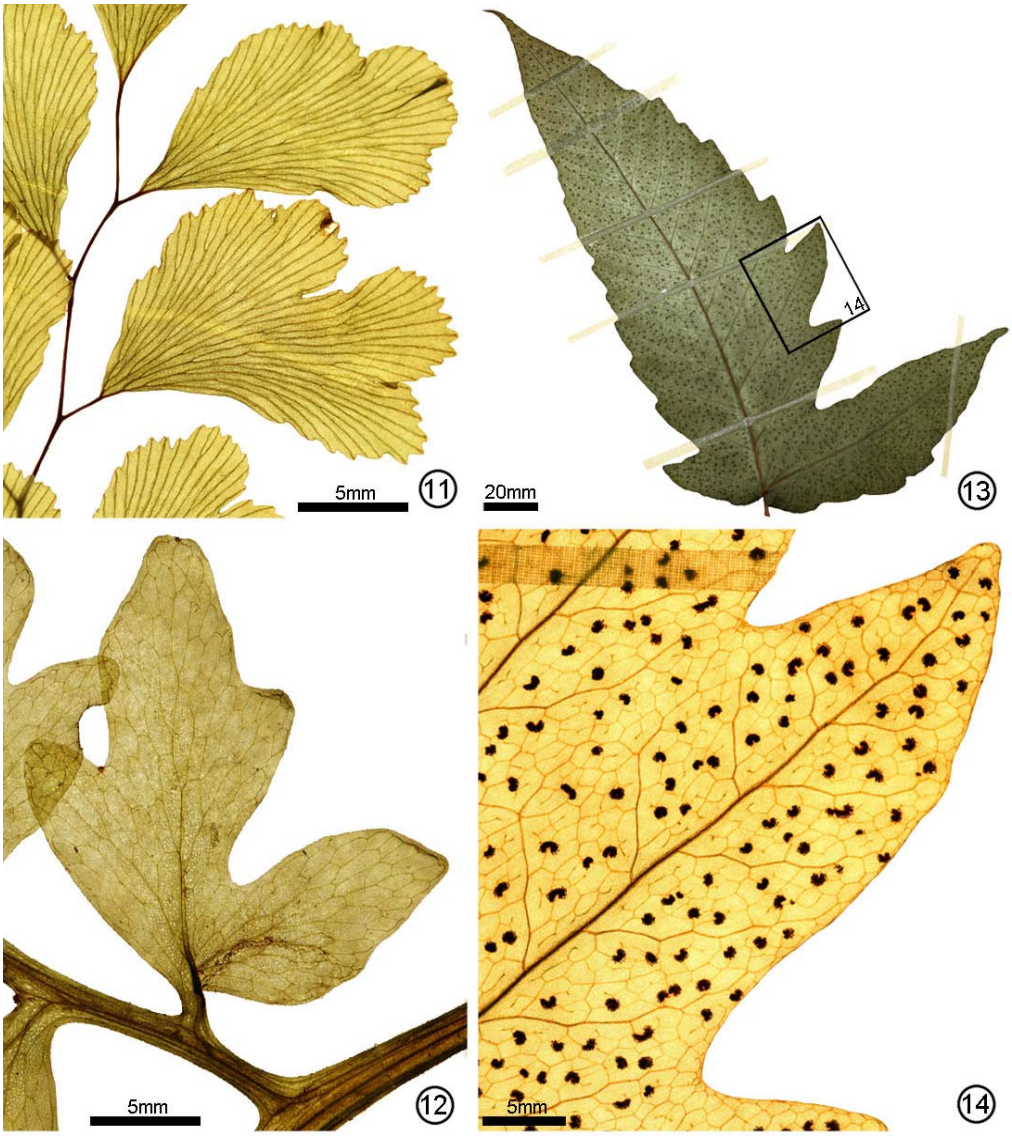
Figure 7. Strict consensus tree showing the position of *Potomacapnos apeleutheron* gen. et sp. nov. associated with the subfamily Fumarioideae. Branch coloring refers to the number of steps under parsimony (morphological character changes) that are required if *P. apeleutheron* is attached to the corresponding branch.



Figures 8–10. Leaflets of three species of extant Fumarioideae. **8,** Trilobed lateral leaflet of *Cysticapnos africanus* US 617339. Note the thickened intramarginal vein near the tooth apex at arrow. Also note that the course and gauge of the primary veins are indistinguishable from the secondary veins and that the areolation is irregular. Scale bar = 5 mm. **9,** Bilobed lateral leaflet of *Trigonocapnos curvipes* US 552984. Note the presence of an intramarginal vein. Scale bar = 5 mm. **10,** Lobed leaflets of *Corydalis micrantha* US 583020. Note alternating asymmetrical lobes and higher vein density compared with leaflets in Figures 8 and 9 . Scale bar = 5 mm.



Figures 11–14. Fern pinnae with features similar to *P. apeleutheron.* **11,** Pinnae of *Adiantum capillus-veneris* US 2201732. The asymmetrically lobed pinnae are borne on a pedate frond. Note the dichotomizing veins that terminate in teeth at the margin. Scale bar = 5 mm. **12,** Pinnule of *Ceratopteris thalyctroides* US 2732636. Note the reticulate venation formed by a single order of veins. Also note the regular pattern of areolation, with areole size decreasing toward the margin and the vegetative bud in the sinus at the lower left of the image. Scale bar = 5 mm. **13,** Lateral pinna of *Tectaria trifoliata* US 534049. Note the large basal lobe, which is basiscopic in the whole frond. Scale bar = 20 mm. **14,** Close-up of *Tectaria trifoliata* US 534049 from the box indicated in Figure 13. Note the hierarchical reticulate venation, freely ending veinlets, and scattered sori. Also note the absence of an intramarginal vein and the absence of glandular structures at the teeth. Scale bar = 5 mm.



Chapter 2: Morphotype catalog of a Zone I (Aptian-earliest Albian) flora from the Fairlington, Virginia, USA

Abstract

Plant fossil collections from Lower Cretaceous floodplain deposits sometimes provide snapshots of local communities that included early herbaceous angiosperms. Here, I describe the plant megafossils in a collection made from the lower part of the Potomac Group near Fairlington, Virginia, USA. The collection includes 123 identifiable plant fossils on 42 hand specimens, comprising nine plant morphotypes: three ferns, five gymnosperms, and one angiosperm. All but one of the described morphotypes also occur in other collections from the lower Potomac Group. There is one moderately abundant angiosperm species in this collection that has been found at other Potomac Group sites, but was incorrectly identified as a fern. Well-preserved specimens of this morphotype clearly show axillary branching, complex leaves, and glandular teeth at the apices of lobes on the leaves; together, these characteristics suggest it was an herbaceous eudicot angiosperm. The one new morphotype in this collection is an enigmatic plant of intermediate abundance and unknown affinity. Based on the simple, pinnate stenophyllous leaves with two vein orders, reticulate secondary veins and the attachment of one leaf to a carbonized axis roughly one centimeter across, I hypothesize that it was a shrubby riparian gymnosperm. This work represents the first step toward a complete morphotype catalog for the flora of the lower Potomac Group.

Introduction

Plant fossil collections from the Potomac Group record part of the rapid diversification of flowering plants during the late Early Cretaceous (Fontaine, 1889; Berry, 1911; Brenner, 1963; Doyle and Hickey, 1976; Hickey and Doyle, 1977). The oldest collections of plant megafossils from the Potomac Group come from Aptian-earliest Albian assemblages (Brenner, 1963; Doyle and Robbins, 1977; Hochuli et al., 2006). The leaves of flowering plants in these assemblages are rare and mostly small. In collections from the middle of the Potomac Group, the leaves of flowering plants show greater diversity of form, are more widely distributed among facies, and angiosperm leaves dominate some collections from crevasse-splay and channel-fill deposits. These observations led to the hypothesis that early flowering plants were primarily herbs and shrubs that colonized bright, disturbance-prone habitats in mesic environments, in other words, they were riparian weeds. From those initial bright, disturbance-prone, near-channel habitats, angiosperm diversity was hypothesized to have spread to a wider variety of habitats such as forest understories and freshwater ponds (Doyle and Hickey 1976; Hickey and Doyle 1977). By contrast, phylogenetic trees in which the extant *Amborella* is the sister group to the rest of angiosperms have been used to infer that the ancestral habitat of crown-group angiosperms may have been wet and shady tropical understories (Feild et al., 2004, 2009), rather than bright and arid "uplands" or bright, mesic riparian corridors on coastal plains (Stebbins, 1965b; Hickey and Doyle, 1977).

Most hypothesis of seed plant phylogeny imply the angiosperm stem lineage had a long Mesozoic history (Mathews et al., 2010), but unequivocal angiosperm

fossils are Cretaceous or younger. The oldest fossils that document the appearance of crown group angiosperms are very rare pollen grains found at sites that would have been at low and middle latitudes during the Hauterivian-Barremian (Hughes et al., 1991; Brenner, 1996). The age of the node that unites crown-group angiosperms is uncertain, but distribution of fossil pollen indicates that the three major clades of angiosperms, the magnoliids, monocots, and eudicots (collectively the mesangiosperms) were distinct by the latest Barremian and probably not much earlier (Doyle, 1992, 2012; Magallón and Castillo, 2009; Doyle and Endress, 2010). Morphologically disparate angiosperm pollen and megafossils occur in Aptian deposits worldwide, indicating that the diversification of crown-group angiosperms was finally underway (Doyle et al., 2008; Mohr et al., 2008; Sun et al., 2011; Barral et al., 2013; Coiffard et al., 2013a; b; Jud and Hickey, 2013).

The flora of Zone I of the Potomac Group post-dates the origin of eudicots, monocots, and magnoliids by several million years. If most of the species in the Zone I flora are in fact eudicots and magnoliids, then the distribution and diversity of angiosperm fossils in the Potomac Group may be primarily a signal of the radiation of mesangiosperms rather than angiosperms as a whole; although ANA-grade angiosperms do appear to be present in the flora (Upchurch, 1984b). New studies of these plant communities as well as the angiosperm species in them will provide important insights on the ecological context of the angiosperm diversification.

Morphotype catalogs express the variety of plant fossils in a flora using a classification system unique to a site, flora, or geologic unit which is independent of the Linnean system (Peppe et al., 2008). The advantage of the morphotype system is

that once operational taxonomic units have been established for a flora, ecological analyses can be applied before the time-consuming process of dealing with taxonomic and systematic descriptions of each entity in a flora is completed (Johnson, 1989). Although morphotypes do not necessarily correspond to Linnean taxa, some morphotypes can be attributed to Linnean taxa either as they are defined or as new information becomes available (Peppe et al., 2008). Here, I present a catalog of morphotypes of the plant megafossils in a collection made by R.W. Brown and Alan Bennison from lower part of the Potomac Group on October 31, 1943 from USGS locality 9030 (Figure 1 and 2). The fossils were collected during the construction of interstate highway 395 "about 0.5 miles south of Cowden, at base of steep slope on south side of new concrete highway out of Fairlington [VA]; south side of Fourmile Run." These fossils have not been published before and were not included in the analyses of Doyle and Hickey (1976) and Hickey and Doyle (1977). The objectives of this work are to present quantitative data on the diversity of a single collection from the lower Potomac Group, to provide descriptions and illustrations of these lower Potomac Group plant fossils, and to extract environmental data since the original outcrop is inaccessible.

Methods

The plant fossils are preserved as adpressions and charcoalified fragments on poorly laminated, light brown mudstone blocks. The fossils were collected from USGS locality 9030 in northern Virginia, USA (Fig. 1) These fossils can be attributed to Zone I of the Potomac Group (Aptian-earliest Albian) based on the locality description and taxonomic similarities with other Zone I collections (Fig. 2). Where

the Arundel Formation (Fm.) is not present in Virginia, the Lower Cretaceous beds are sometimes referred to as the Potomac Fm. and are roughly equivalent to the Patuxent Fm. (lower Zone I) in Maryland. All of the specimens are curated in the Department of Paleobiology at the National Museum of Natural History, Smithsonian Institution, Washington DC, USA.

I numbered all of the blocks in the collection, and assigned decimal numbers to specimens of interest on blocks (e.g. block 11 bears fossil specimens 11.1 and 11.2). Then, I sorted the plant fossils into three broad taxonomic categories (ferns, gymnosperms, and angiosperms) and grouped the shoots and leaves into morphotypes by leaf architecture (Ellis et al., 2009) (Table 1). I assigned each morphotype an informal designation beginning with the letters PA, referring to the Patuxent and Arundel Formations, which comprise the lower part of the Potomac Group in Maryland. I provide photographs and descriptions of each morphotype, and include some synonymies to aid in comparison with other Potomac Group collections. I photographed the specimens using a Canon EOS digital camera with a 100mm EF macro lens and processed the images with whole-image manipulations such as the adjust levels tool and the Auto Color tool using Adobe Photoshop (San Jose, California, USA).

Format of descriptions.

Morphotype code (PA#).
Figure #
Name

Systematic affinity:

Description:

Exemplar:

Discussion:

Description of Morphotypes

Ferns

Morphotype: PA1
Figure 3.
Sectilopteris sp. Miller and Hickey, 2008

Systematic affinity: Class Polypodiopsida; Order incertae sedis (cf. Schizaeales); Family incertae sedis; Genus *Sectilopteris* Miller et Hickey 2008

Description: Frond fragments sterile and at least bipinnate, anadromous; rachilla course straight. Pinnae alternate, >20mm long, 2mm wide, costa straight, attachment decurrent, forming an acute angle to rachilla. Pinnules pinnatisect, alternate, width <1mm, length 2-3mm, narrowly elliptic to obovate, apex rounded, base broadly attached to rachilla, diverging from rachilla at an acute angle. Pinnule length <4mm, pinnule shape elliptic to obovate, basiscopic pinnule margin decurrent, margin irregularly toothed. Venation dichotomous, without midvein, without reticulation; veins appear to end freely at the margin. Cuticle not visible under florescence microscopy.

Exemplar: 9030-37.1

Discussion: Fossils of ferns like *Sectilopteris* are widespread throughout Cretaceous deposits worldwide (Miller and Hickey, 2008). *Sectilopteris* is a genus for ferns (Polypodiopsida) of indeterminate affinity, but likely includes many members of Schizaeaceae and Cyatheaceae. The characteristic features of *Sectilopteris* are fronds at least bipinnate fronds with narrow, acutely attached pinnules that have dichotomizing venation and without midveins (Miller and Hickey, 2008). The acute, narrow pinnules distinguish this morphotype from others in this collection.

Morphotype: PA2
Figure 4.
Furcillopteris sp. Miller and Hickey, 2008

Systematic affinity: Class Polypodiopsida; Order and Family incertae sedis; Genus *Furcillopteris* Miller et Hickey 2008

Description: Single fragment of a sterile fern pinnule. Pinnule attachment to rachilla unknown, but likely pinnate. Pinnule length unknown, pinnule width 3mm; margin smooth, base appears truncate, apex unknown. Venation open, no reticulation; midvein distinct with pinnately arranged lateral veins; lateral veins depart at angle of 50 degrees, fork once near the midvein and terminate at edge of the pinnule. Seven lateral veins terminate along 2.5mm of pinnule margin. Cuticle not visible under florescence microscopy.

Exemplar: 9030-11.1

Discussion. This genus is used for vegetative fern foliage similar to *Cladophlebis*, but for which the mode of attachment to the rachis or rachilla is unknown. Only a single specimen assignable to this genus occurs in the collection. It is clearly not a fragment of another better known morphotype in the collection because the pinnate venation with forked lateral veins is distinct.

Morphotype PA3
Figure 5
Acrostichopteris densifolia Fontaine 1889

Systematic affinity: Class Polypodiopsida; Order and Family incertae sedis; Genus *Acrostichopteris* Fontaine 1889

Description: Single fragment of a sterile, at least once pinnate frond. Rachilla winged. pinnules small, alternate, flabellate, lobed and toothed; each pinnule is divided once into two major lobes, and each of those once into two secondary lobes and each of those is divided once into two tertiary lobes; pinnule sinuses acute; pinnule base acute; basicopic margin decurrent on the rachilla; course of the basiscopic margins basally recurved until roughly perpendicular to the rachilla. Tertiary lobes terminate in one or two simple acute teeth. A single vein departs the rachilla and enters each pinnule at an angle of about 30 degrees and dichotomizes at angles of 20-25 degrees up to four times. Pinnule venation open, dichotomizing, no reticulation. Veins terminate in simple marginal teeth. Cuticle not visible under florescence microscopy.

Exemplar: 9030-24.2

Discussion: Ferns of the genus *Acrostichopteris* are widespread in Lower Cretaceous deposits (Sender et al., 2005; Herman et al., 2012). Preliminary work on some fertile specimens of *Acrostichopteris* from the Potomac Group suggests a close relationship with Schizaeales (Skog, 1995). Ferns in the genus *Acrostichopteris* are characterized by winged rachillae and decurrent, flabellate pinnules with acute teeth at the tips of the lobes. The species *A. densifolia* is characterized by small pinnules that are densely crowded to slightly overlapping, l:w less than 2:1, and pinnules generally dissected into three orders of lobes (Fontaine, 1889). Within this collection, this morphotype may be distinguished by the flabellate pinnules and winged rachilla.

Gymnosperms

Morphotype PA4
Figure 6
Dioonites buchianus (Ettingshausen) Bornemann 1856.

Systematic affinity: Class Pinopsida; Order Bennettitales; Family Williamsoniaceae; Genus *Dioonites* Miquel 1851

Description: Single specimen of a small frond; leaf pinnately compound. Leaf length ~9 cm, width at least 6 cm; rachis 1.5mm wide. Leaflets subopposite; shape linear-ovate; leaflet length 3-4cm, width 2mm; leaflet apex acute, straight; leaflet base slightly constricted, broadly attached to rachis, with decurrent basicopic margin.

Venation not reticulate, parallel. Margin entire. Cuticle not visible under florescence microscopy.

Exemplar: 9030-33.1

Discussion: This specimen is smaller than most specimens of *Dioonites buchianus* from other Zone I collections; however in all other aspects such as leaflet shape and leaflet attachment to the rachis it conforms to *Dioonites*. Thus, it may simply be an unusually small leaf from this abundant species, rather than a distinct species represented by only one remarkably complete specimen. The absence of larger fragments of *Dioonites* from this collection may be the result of collecting bias in the field.

Morphotype: PA5
Figure 4
Pagiophyllum sp. Heer 1881

Systematic affinity: Class Pinopsida; Order Pinales; Family incertae sedis; Genus *Pagiophyllum* Heer 1881

Description: Isolated conifer shoots. Shoot mostly curvilinear, width up to 0.5 cm; main axis width up to approximately 2.5 mm. Leaves persistent, divergent from stem, helically arranged. Length of the free portion of the leaf longer than the width of the cushion, width approximately 2 mm, length up to 5mm. Leaf base decurrent and not contracted, clasping the stem; leaf apex acute; leaf margins entire. Venation not visible. Cuticle not visible under florescence microscopy.

Exemplar: 9030-11.2

Discussion: I follow Miller and Hickey (2010) in applying the generic name *Pagiophyllum* to isolated conifer shoots with helically arranged, persistent, falcate leaves with uncontracted and decurrent bases, acute tips, entire margins, and inconspicuous veins. Some of the *Pagiophyllum* shoot fragments in this collection are three-dimensionally preserved charcoalified fragments.

Morphotype: PA6
Figure 8
Pityocladus sp. Seward 1919

Systematic affinity: Class Pinopsida; Order Pinales; Family Pinaceae; Genus *Pityocladus* Seward 1919

Description: Branched conifer shoot with long shoot-short shoot organization. Long shoot straight, bearing five alternately arranged short shoots, short shoots bearing helically arranged leaves. Long shoot ~6cm long, ~2.2 mm wide; short shoots 4-5 mm long, ~2.2 mm wide. Leaves linear, >2cm long, 0.5 mm wide; with a single vein and entire margins. Cuticle not visible under florescence microscopy.

Exemplar: 9030-2.1

Discussion: The genus *Pityocladus* is used for vegetative shoots similar to *Cedrus*, *Larix*, and *Schizolepis.* The type material of *Pityocladus* was found in association with *Schizolepis* cones (Nathorst, 1897; Seward 1919). There are no pinaceaous cones in this collection; so I apply the genus *Pityocladus* to this morphotypes following the recommendation of Seward (1919).

Morphotype: PA7
Figure 9
Podozamites angustifolia (Fontaine) Jud comb. nov.

Systematic affinity: Class: Pinopsida; Order Pinales; Family incertae sedis; Genus *Podozamites* Braun 1843

Description: Unbranched stem with attached leaves. Shoot incomplete; length >6.6 cm; width including leaves, >6 cm; width of stem approximately 0.5 cm. Leaves subopposite to alternately arranged (helical) on the shoot, attached at a 30° to 55° angle to the shoot axis, plagiotropic; leaves lanceolate; margins linear; length >3.7cm; width 0.35 to 0.4 cm, l/w ratio greater than or equal to 10:1; leaf spacing 0.9 to 1.3 cm; leaf apices not preserved on this specimen; base straight symmetrical, attached by a short stalk, approximately 1-2 mm long and appearing twisted in some specimens, possibly as a result of the planation of helically arranged leaves; margins entire; resin bodies absent. Venation in one order, parallel, with ~8 veins in the midsection of the leaf. Cuticle not visible under florescence microscopy.

Exemplar: 9030-1.1

Discussion: I follow Miller and Hickey (2010) in considering *Nageiopsis* Fontaine a junior synonym of *Podozamites* Braun 1843 because the slight difference in the arrangement of leaves along the stem in adpression and the convergence of the veins at the apex of the leaves are insufficient to distinguish *Nageiopsis* from *Podozamites*. The specimens described here match specimens described as *Nageiopsis angustifolia* in other Potomac Group collections by Fontaine (1889: pg. 202 pl. 86, figs. 8, 9; pl. 87 figs 2-6; pl. 88, figs 1, 3, 4,6-8; pl. 89 fig. 2.); these specimens should be transferred to the genus *Podozamites.* Leafy shoots assigned to the genus *Podozamites* are most similar to Araucariaceae and Podocarpaceae. These families comprise a monophyletic group with respect to the remaining living extant conifer genera (Rai et al., 2008; Leslie et al., 2012).

Morphotype PA8
Figures 9-12

Systematic affinity: Class, Order, and Family *incertae sedis*

Description: Axis diameter ~7mm; leaf attachment petiolate; petiole winged, 3mm wide; petiole attachment marginal. Leaf size notophyll. Leaf simple, unlobed, symmetrical and ovate-elliptic, possibly linear. Length >5cm, width 1.6-2 cm. Apex angle acute; base angle acute, base shape decurrent; margins entire; midvein pinnate; second-order veins decurrent to the midvein; and forming an irregular reticulum of low angle anastomoses toward the margin of the leaf; spacing constant, angle of

origin about 30° and the veins recurve basally so that near the margin of the leaf the angle of the secondary veins to the primary vein is roughly 50-60°. Secondary veins terminate at an intramarginal collecting vein. Areoles elongate. Cuticle not visible under florescence microscopy. One specimen in the collection was preserved with a petiole attached to an elongate axis ~7mm in diameter with long internodes, but unfortunately this connection was broken during preparation and the fragment of the coalified stem mostly disintegrated (not photographed).

Exemplars: 9030-32.1-3

Discussion: The blade of this morphotype looks superficially similar to that of *Glossopteris* and *Mexiglossa* leaves and to the leaflets of *Sagenopteris*; however, this morphotype can be distinguished from these genera based on the presence of an intramarginal commissural vein, whereas the former three genera have veins that end freely at the margin (Harris, 1964). Furthermore, the simple, petiolate leaves of this morphotype are distinct from the simple sessile leaves of *Glossopteris* and *Mexiglossa*, and from the palmately compound leaves of *Sagenopteris*, which have an unwinged petiole. The attachment of this simple leaf to a stem with long internodes in this morphotype suggests the herbaceous or shrubby habit of a seed plant rather than a fern, because fern stipes are typically crowded along the stem (e,g, ferns usually have short internodes). It is unlikely that this morphotype is an angiosperm because there are only two orders of venation, and the reticulum of minor veins forms elongate areoles. This species most likely represents an extinct gymnosperm lineage not

described from other Potomac Group collections. This is also the only morphotypes on which I observed evidence of insect damage (Fig. 12). It occurs as small holes surrounded by dark reaction tissue.

Angiosperms

Morphotype: PA9

Figure 13

"Sphenopteris" thyrsopteroides Fontaine (1889):89, pl 25, fig. 3; pl 58, fig 5

Systematic affinity: Class Magnoliopsida; Order incertae sedis (cf. Ranunculales, Proteales); Family incertae sedis

Description: Small, much-branched herbaceous shoots with attached leaves and fibrous adventitious roots. Fibrous adventitious roots produced in pairs at nodes. Stems flexuous. Branching axillary, buds occasionally visible in the axils of the leaves. Leaves helically arranged (alternate) along the stem. Leaf attachment petiolate, petioles short (≤5mm), petiole base clasping and without stipules. Petiole attachment marginal. Leaf size leptophyll; blade organization variable, overall laminar shape ovate; roughly twice pinnately lobed; lobe size and sinus depth decreases smoothly toward the apex; secondary lobes alternate and anadromous. Laminar L:W ratio 1-1.25:1; apex obtuse, rounded; base obtuse, concave to decurrent, and base insertion usually slightly asymmetrical. Primary venation pinnate to nearly palmate with three primary veins; major secondary veins craspedodromous; secondary vein spacing decreases distally, secondary vein angle also smoothly decreases proximally; minor secondary veins craspedodromous; tertiary vein network

not visible. Teeth vascularized by a medial principal vein that terminates at the apex of the tooth and thickened lateral accessory veins continuous with a faint perimarginal vein; tooth apices papillate. Cuticle not visible under florescence microscopy.

Exemplar: 9030-22.1

Discussion: This species is widespread among Zone I Potomac Group collections. This species is clearly not a fern because the fossils show axillary branching and glandular (papillate) teeth. The herbaceous habit and glandular teeth indicate a relationship to eudicot angiosperms rather than gymnosperms. A formal diagnosis and discussion of the significance of this species will follow in another manuscript.

Discussion

The USGS 9030 collection comprises 42 blocks and 123 identifiable plant fragments that I have attributed to nine species (Table 1): three ferns, one cycadophyte, three conifers, one broad-leaved gymnosperm of unknown affinity, and one herbaceous angiosperm. Although I have assigned a morphotype code to each entity in the collection, I have opted to use the Linnean name for morphotypes where I was able to determine the genus or species. The conifer *Pagiophyllum* sp. is represented by the most specimens in the collection, often occurring on blocks where it was clearly not the specimen of interest. Four morphotypes are represented by a single specimen: one fern, one cycad and two conifers. The relatively complete specimens of *Dioonites, Podozamites,* and *Pityocladus* in the museum collection

suggest that these were chosen from among a larger number of specimens in the field, and thus that the relative abundance of these species was higher. Therefore, this collection probably represents a small fraction of the plant fossils encountered when the collection was made.

The fossils are preserved in a fine-grained bed, or possibly beds, with little or no lamination. Beds like this are typical of overbanks deposits and crevasse-splay deposits in the lower Potomac Group (Fontaine, 1889; Upchurch and Doyle, 1981; Jud and Hickey, 2013). The preservation of herbaceous angiosperms with attached stems, leaves, and roots in the fine grained matrix suggests minimal transport prior to preservation in topographic lows. An abandoned channel setting appears likely because some of the plants appear to be adapted to bright, channel margin habitats, such as the stenophyllous PA8 and the small-leaved angiosperm herb PA9. The abundance of charcoalified conifer (*Pagiophyllum*) shoots suggests that in addition to overbank floods or channel avulsion events, disturbance by fire was a common form of disturbance in this community.

The sedimentological context of this collection and the preservation of attached organs indicate that the fossils in this assemblage were not transported far prior to preservation. Together with the sedimentology, the species diversity and relative abundance of plant megafossils in this collection indicate that this assemblage probably represents a snapshot of the plant community that was growing in or near an abandoned channel in a conifer-dominated and disturbance-prone riparian community. Ferns, angiosperms, and gymnosperms of small stature formed the understory. In the future, this morphotype catalog can serve as a basis for the

development of a larger and more refined morphotype catalog for the Potomac Group Zone 1 flora.

Tables and Figures

Table 1: Rank abundance of each morphotype in the collection. Note that the rank abundance is slightly different if measured by identifiable fragment versus by occurrence on blocks. *These morphotypes are likely under-represented in the collection, and therefore their rank abundance is underestimated.

Morphotype	Name	Systematic affinity	Exemplar	Fragments	Blocks
PA5	*Pagiophyllum sp.*	Conifer	9030-11.2	77	24
PA8		unknown	9030-32.1-3	17	6
PA9	*"Sphenopteris" thyrsopteroides*	Angiosperm	9030-22.1	16	8
PA1	*Sectilopteris sp.*	Fern	9030-37.1	8	7
PA2	*Furcillopteris sp.*	Fern	9030-11.1	1	1
PA3	*Acrostichopteris densifolia*	Fern	9030-24.2	1	1
PA4	*Dioonites buchianus*	Bennettitales	9030-33.1	1*	1
PA6	*Pityocladus sp.*	Conifer	9030-2.1	1*	1
PA7	*Podozamites angustifolia*	Conifer	9030-1.1	1*	1

Figure 1: Map of the Potomac Group outcrop area in the eastern United States. Note the location of the site where these fossils were collected at arrow.

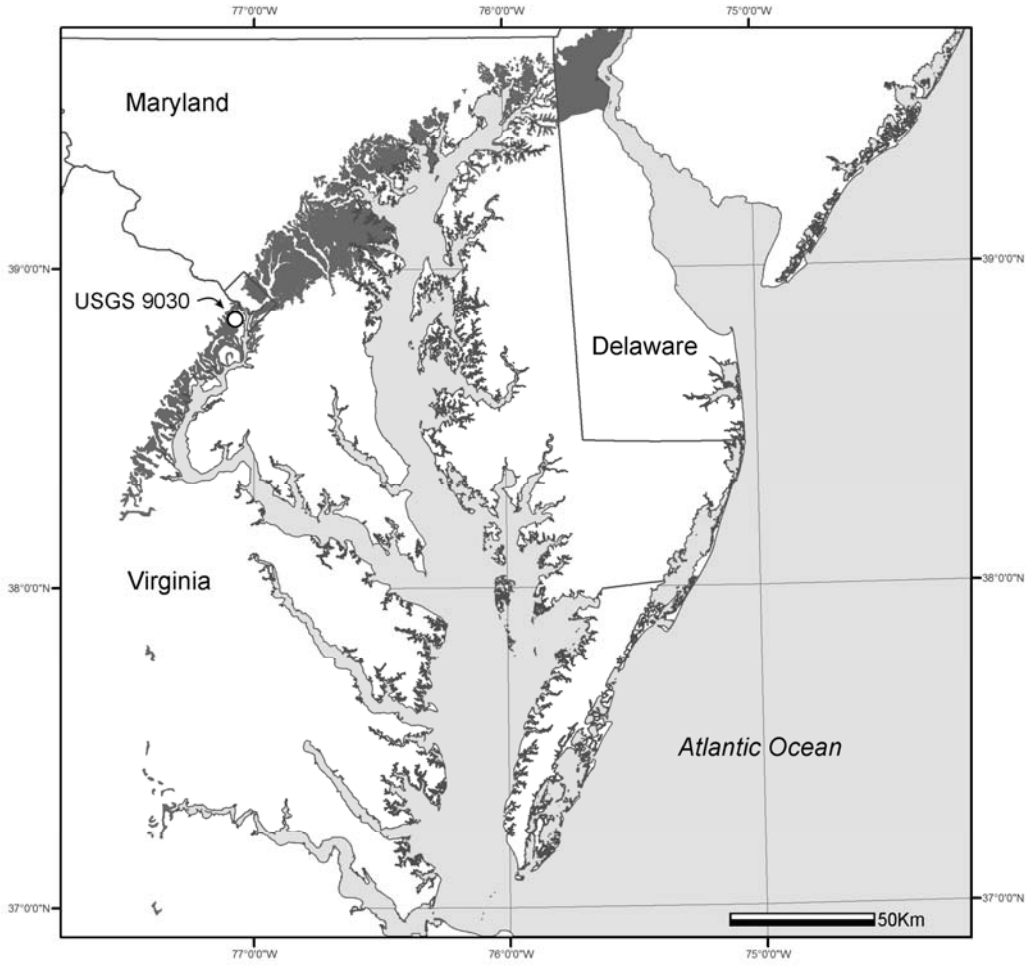


Figure 2: Age of the lower part of the Potomac Group (modified from Doyle et al. (1992) and Hochuli et al. (2006)). The dates on the left are from Gradstein et al. (2012). This collection most likely comes from the lower part of Zone I based on the locality description, but an upper Zone I position is not ruled out.

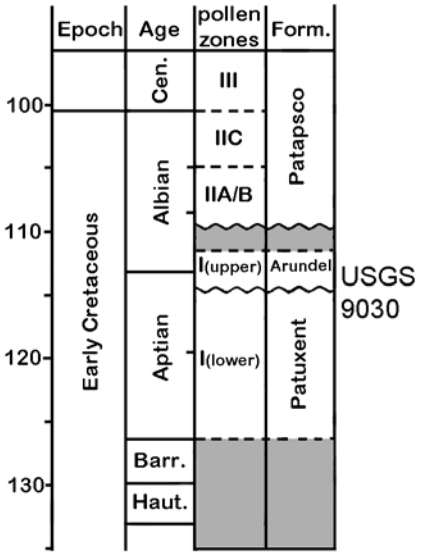


Figure 3: Morphotype PA1, *Sectilopteris* sp., twice pinnate fragment of fern frond. Scale bar = 1cm. **Figure 4.** Morphotype PA2, *Furcillopteris* sp. at arrow; Morphotype PA5 *Pagiophyllum* sp. at center. Scale bar = 5mm. **Figure 5**: Morphotype PA3, *Acrostichopteris densifolia*; fragment of pinnate frond showing lobed, flabellate pinnae. Scale bar = 5mm.

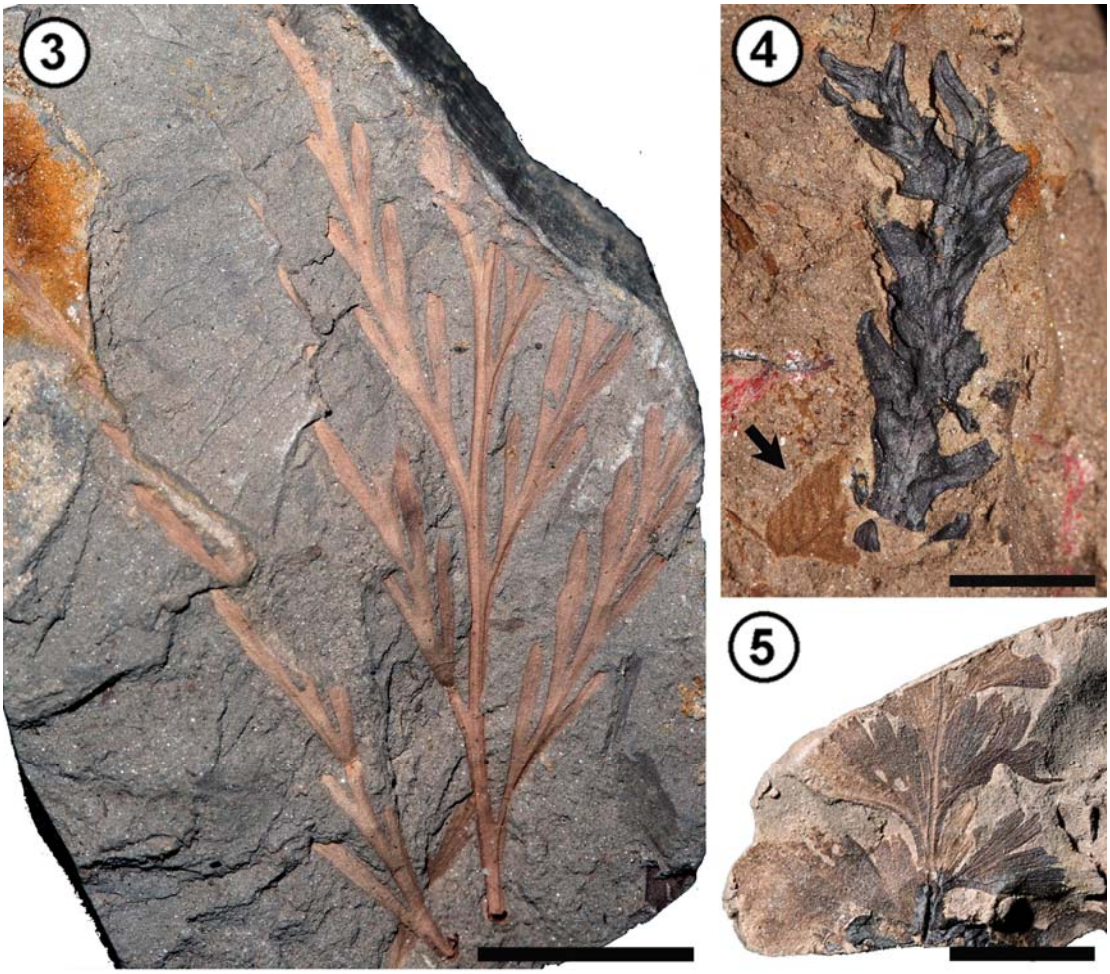


Figure 6: Morphotype PA4, *Dioonites buchianus*; nearly complete frond. Scale bar = 1cm. **Figure 7**: Morphotype PA6 *Pityocladus sp.*; long shoot with attached leafy short shoots. Scale bar = 1cm.

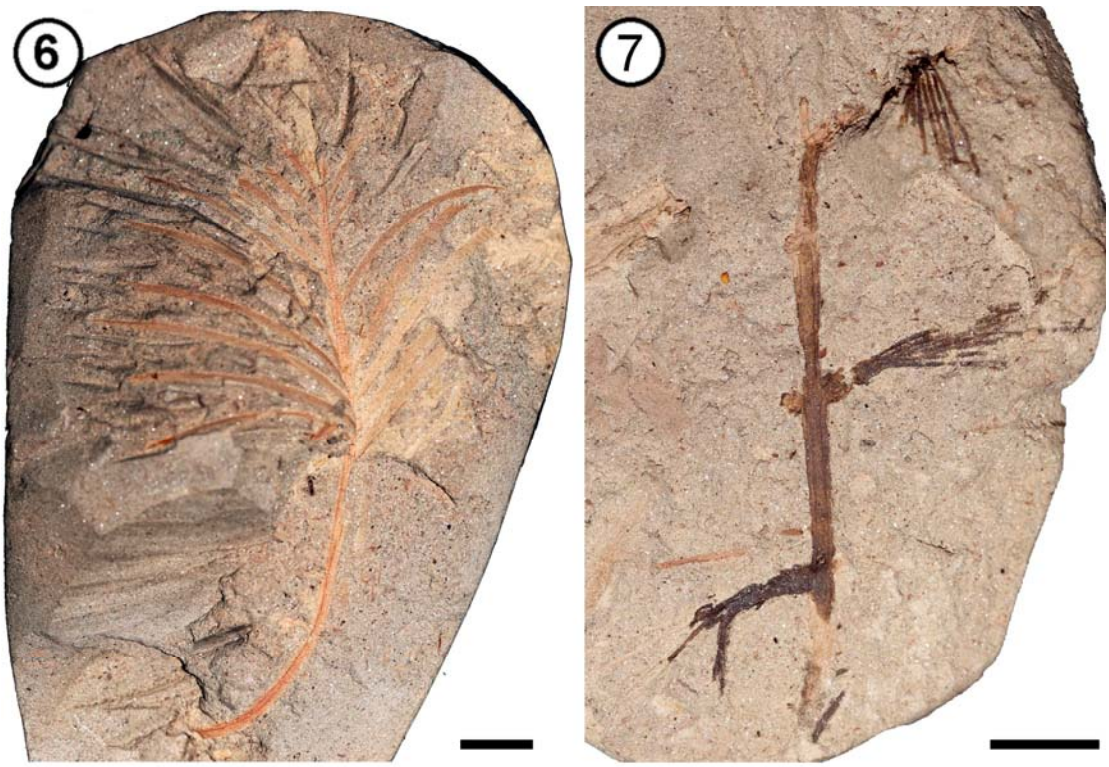


Figure 8: Morphotype PA7 *Podozamites angustifolia;* long shoot with helically arranged and planted leaves. Scale bar = 1cm

Figure 9: Line drawing of a base and incompletely preserved apex of Morphotype PA8. Scale bar = 5mm

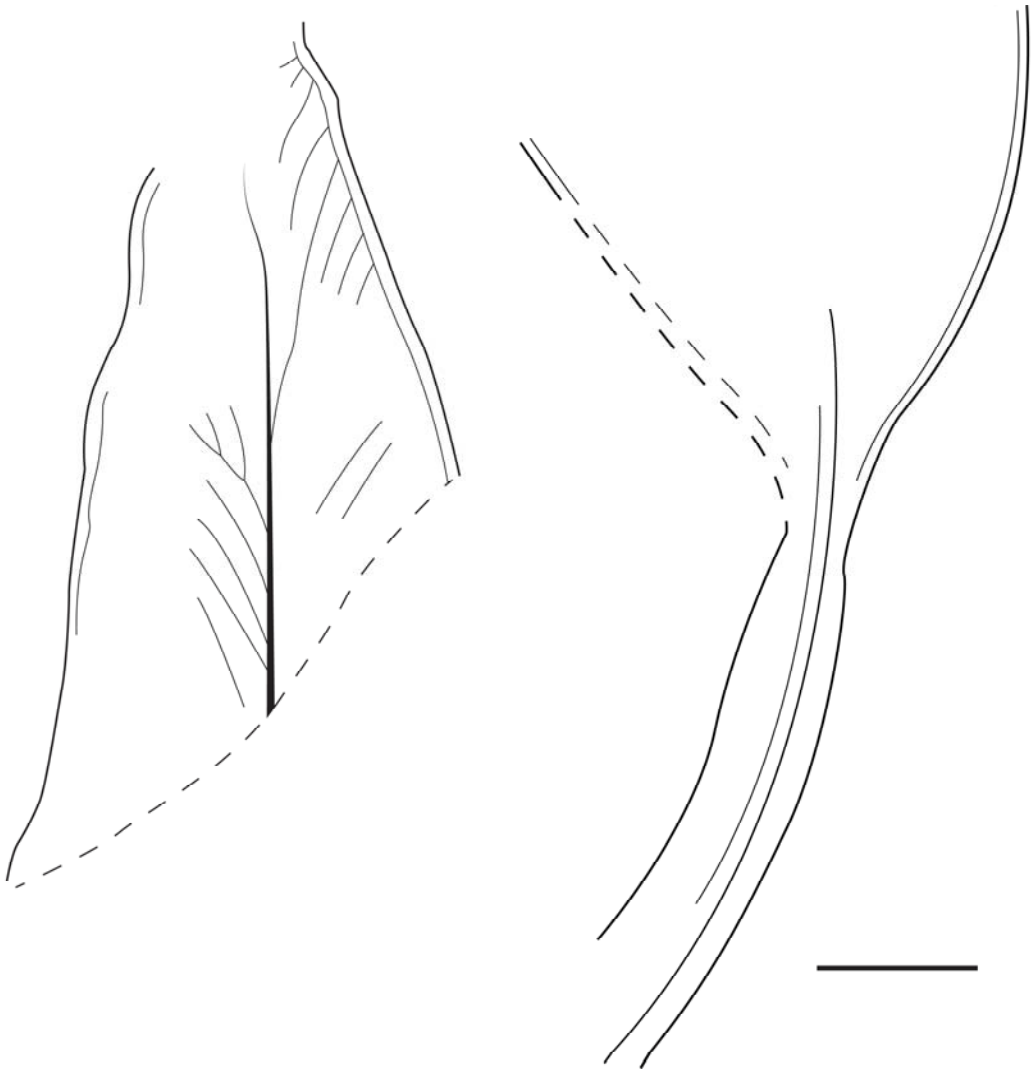


Figure 10: Morphotype PA8 Incompletely preserved apex, as illustrated in Figure 9. Scale bar = 5mm. **Figure 11**: Morphotype PA8 Close up of PA8 specimen showing rare reticulations at arrows. Scale bar = 2mm. **Figure 12**: Insect damage on Morphotype PA8. Hole feeding (black arrows) and leaf margin feeding (white arrow) damage with reaction tissue preserved as a dark margin. Scale bar = 5mm

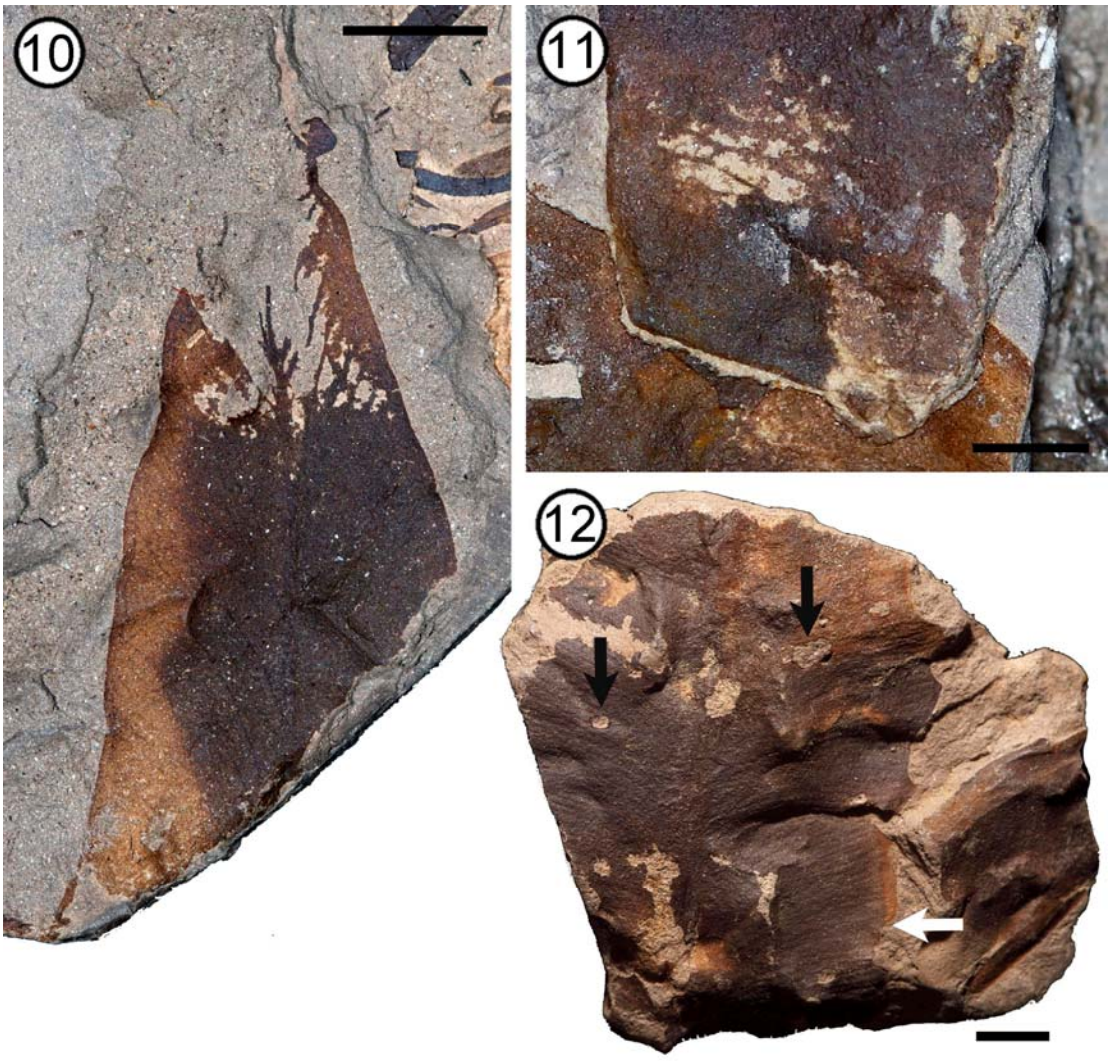


Figure 13: Morphotype PA9 "*Sphenopteris*" *thyrsopteroides*; leafy shoots of the herbaceous angiosperm. Scale bar = 5mm

Chapter 3: Morphology and ecology of an herbaceous angiosperm from the Lower Cretaceous of eastern North America

Abstract

•*Premise of the study*: The diversity of form and ecological strategy among modern flowering plants suggests that there are likely many reasons for their ecological success. Clarifying the most important mechanisms during the initial diversification of angiosperms requires the study of Early Cretaceous fossils. This is because extinction has eliminated much of the evidence of early angiosperm diversity and because the many modern lineages have acquired derived traits through convergent evolution. Here, I describe a species of angiosperm that lived during the Early Cretaceous in eastern North America. I discuss the phylogenetic position, growth habit, life history and habitat of this species; and I discuss implications of this species for current models of early angiosperm ecology and evolution in general.

•*Methods*: The fossils discussed here were collected over the last c.135 years from Aptian and early Albian deposits in the Potomac Group (Maryland and Virginia, USA), and are reposited in the Department of Paleobiology (National Museum of Natural History, Smithsonian Institution) and the Peabody Museum of Natural History (Yale University). Some specimens were previously described as ferns, and others were unidentified. I prepared, described and photographed the specimens using standard methods, and compared them with similar extant and fossil plants.

•*Key results*: The plant, *Fairlingtonia thyrsopteroides* comb. nov. (Fontaine) Jud, was a creeping herbaceous angiosperm with minute, deeply dissected leaves and glandular chloranthoid teeth. It may be most closely related to eudicots, or may belong below the split between monocots and eudicots. The fossils commonly occur as attached leaves and axes in thin beds of fine-grained sediment that alternate with poorly sorted sandstones. I infer preservation with little or no transport in near-channel low-energy crevasse-splay deposits. Plant habit, leaf architecture, and sedimentary environment indicate that this plant was adapted to colonizing disturbance-prone bright and wet substrates along humid riparian corridors.

•*Conclusions*: This species is now the most completely known and widespread angiosperm from the Aptian portion of the Potomac Group. These fossils confirm that herbaceous angiosperms adapted to colonizing bright, disturbance-prone, humid riparian habitats were widespread in subtropical eastern North America early in angiosperm evolution. Rapid evolution and high speciation rates have been linked to small size and the herbaceous habit, which are common attributes in early angiosperms. These life history features may have been important in the rapid early diversification of angiosperms, before they became dominant contributors to vegetation cover globally.

Introduction

The ecological factors associated with the angiosperm diversification during the Early Cretaceous (Hauterivian-Albian) remain obscure. Two well-known hypotheses about angiosperm ecology in the Early Cretaceous are the "riparian weed" model and the "ancestral xerophobia" model. The riparian weed model suggests that

Early Cretaceous angiosperms were mostly small, fast-growing, disturbance-adapted herbs and shrubs that colonized bright, riparian habitats along coastal plains (Hickey and Doyle, 1977; Retallack and Dilcher, 1986; Taylor and Hickey, 1996; Wing and Boucher, 1998; Royer et al., 2010). This idea is supported by the sedimentary environments in which many early angiosperm fossils have been found, as well as ecological inferences from the morphology of fossil leaves. The ancestral xerophobia model proposes that the ancestors of crown-group angiosperms were drought-intolerant shrubs that colonized wet, disturbance-prone microsites in shady forest understories. This idea comes primarily from the comparative biology of extant plants that belong to the ANA (*Amborella*-Nymphaeales-Austrobaileyales) grade of early-diverging angiosperm lineages, as well as Chloranthaceae. A re-evaluation of select early angiosperm fossils including *Ficophyllum* and dispersed cuticles (Upchurch, 1984b; Feild et al., 2004, 2009) provides some support for this model. However, there is virtually no fossil record of Early Cretaceous angiosperms from wet, tropical understories that would corroborate this model (Feild et al., 2004).

Although these two models have been treated as alternatives, they address two slightly different questions. The first is an ecological question: What kinds of plants were the most diverse and widespread, and therefore most likely to be preserved, early in angiosperm history? The second is phylogenetic: What kind of plant was the last common ancestor of a given angiosperm clade (e.g. crown-group angiosperms)? The first question could be addressed by evaluating the morphology, diversity, and distribution of angiosperm fossils in Lower Cretaceous deposits (Royer et al., 2010), whereas the second could be addressed by evaluating both living and fossil plants in a

phylogenetic context and determining the influence of additional species on ancestral state reconstructions.

Here I describe a common fossil angiosperm from the Lower Cretaceous of eastern North America that is often preserved with stems, leaves, and roots attached. I discuss its phylogenetic position, use functional traits and sedimentological context to draw conclusions about its autecology, and consider its implications for the two models of early angiosperm ecology and evolution.

Methods

Geologic and Depositional Setting

The fossils are preserved as compressions and were collected from at least eight localities in Maryland and Virginia, USA in the Lower Cretaceous Potomac Group (Figure 1). Dispersed pollen and spore assemblages have been used to subdivide the Potomac Group into informal stratigraphic zones and subzones (Brenner, 1963; Doyle and Robbins, 1977). All of the fossils occur in fine-grained fluvial beds (claystone, mudstone) of Zone I, which typically alternate with poorly sorted coarse beds (Fontaine, 1889). Zone I is divided into a lower, Aptian part and an upper, latest Aptian-early Albian part based on lithology and the presence of certain palynomorphs in the upper part, including tricolpate pollen. The relationship between upper and lower units of Zone I are often simplified. Arundel Clay deposits are discontinuous bodies at or near the top of the Patuxent Formation, and the disconformities separating upper and lower Zone I are of unknown duration (Kranz, 1998). The fossils described here were collected from both the upper and lower Zone I (Figure 2). Zone I of the Potomac Group comprises fluvial deposits ranging from massive

claystone, to cross-bedded sandstone, to matrix supported cobble-conglomerates (Hickey and Doyle, 1977; Upchurch and Doyle, 1981; Jud and Hickey, 2013). These depositional end-members indicate a wide range of flow regimes typical of regions with seasonal rainfall or extreme weather events (Blum and Törnqvist, 2000). Based on sedimentary evidence and paleoclimate models the climate of the Potomac basin is thought to have been humid subtropical (Upchurch and Wolfe, 1987; Beerling and Woodward, 2001; Fluteau et al., 2007).

Fossil Preparation

The fossils are curated in the Department of Paleobiology at the National Museum of Natural History, Smithsonian Institution in Washington D.C. and the Yale Peabody Museum in New Haven, Connecticut. The fossils are preserved as carbonaceous compressions, but I did not see cuticular details under epiflorescence microscopy. Some of the fossils were prepared by degaging, but others required no new preparation. I photographed the fossils using a Canon EOS digital camera with a 100mm EF macro lens and a Nikon D70 digital camera with a Macro-Nikkor 65mm lens. I processed images with Adobe Photoshop (San Jose, California, USA) and improved contrast by adjusting "levels" and by using the Auto Color option. I performed further whole-image manipulations of color on photographs of specimens that have faded and are difficult to see. The leaf architectural character definitions I use are based on those outlined in the *Manual of Leaf Architecture* (Ellis et al., 2009) with some of the modifications developed by Jud and Hickey (Jud and Hickey, 2013). I measured leaf area and petiole width from photos of seven complete or nearly

complete leaves for which the total area of the blade could be estimated using the AnalyzingDigitalImages software.

Systematics

Class–Embryopsida Pirani & Prado 2012

unranked– Euphyllophytes

unranked– Spermatophytes (Seed plants)

unranked– Angiosperms (Flowering plants)

unranked– Eudicot clade (Tricolpates)

Order– Unknown

Family– Unknown

Genus–Fairlingtonia gen. nov.

Species– Fairlingtonia thyrsopteroides (Fontaine) comb. nov. (Figs. 3-11)

Sphenopteris thyrsopteroides Fontaine 1889 pg. 89 pl. 25 fig. 3 & pl. 58 fig. 5

Sphenopteris spatulata Fontaine 1889 pg. 93 pl. 50 fig. 4

Sphenopteris pachyphylla Fontaine 1889 pg. 93 pl. 50 fig. 5 (Fig. 4)

Thyrsopteris pachyphylla Fontaine 1889 pg. 135 pl. 50 fig. 3

Emended generic diagnosis–Small, stoloniferous herbs with axillary branching and fibrous adventitious roots produced in pairs at nodes. Leaves alternate (one per node, at least tristichous, but difficult to determine in compression). Resting buds occasionally visible in leaf axils. Leaf attachment petiolate, petioles short (≤5mm), petiole base without stipules and decurrent to stem. Petiole width narrows toward blade of leaf. Blade attachment marginal. Leaf size leptophyll, blade ovate and deeply dissected. Apex obtuse, rounded, often slightly asymmetrical. Base obtuse, but not

reflex, often slightly asymmetrical. Leaf dissection varies from trifoliate with pinnately arranged secondary lobes to twice pinnately lobed. Sinuses rounded. Lobe size and sinus depth both decrease acropetally such that lobes and teeth intergrade. Lateral pair of leaflets or basal-most primary lobes has alternate secondary lobes that develop acropetally. First and basal most secondary lobe is along acroscopic margin of primary lobe or lateral leaflet (=anadromous of pteridology). Major (i.e. primary, secondary, and minor secondary) veins craspedodromous. Intramarginal secondary vein present. Tertiary veins fine, irregular reticulate, areolation poorly developed, freely ending veinlets not present. Glandular teeth with papillate apices at apices of lobes supplied by a medial principle vein and laterally by thickened intramarginal veins.

Emended specific diagnosis– Stems 1-3mm in diameter, stoloniferous, and much-branched. Internodes generally ≤5mm. Petioles 2-5mm long. Blade up to 10mm long, by up to ~13mm across (but usually much less); leaf area <70 mm^2; petiole width 0.4-0.7mm at attachment to the blade.

Holotype–USNM 597566 (Figure 3) is curated in the type collection in the Department of Paleobiology, National Museum of Natural History, Washington D.C. This specimen was illustrated by Fontaine in 1889 (Plate XXV Fig. 3, LVIII Fig, 5); however, the specimen is severely faded and the original illustrations convey the interpretation of this plant as a fragment of a fern frond, rather than a branching shoot. Other specimens from the same collection or different collections were housed in the stratigraphic collections.

Paratypes–USNM 597567, shoot (Figure 4); USNM 597568, shoot (Figure 5); USNM 597569, leaf (Figure 6); USNM 597570, shoot (Figure 7); USNM 597571, shoot (Figure 8); USNM 597572, shoots of *Fairlingtonia thyrsopteroides* mixed with fragments of the fern *Acrostichopteris sp.* (Figure 9); USNM 597573, shoot with attached fibrous adventitious roots (Figure 10); YPM 60054a&b, shoot showing venation of the leaves (Figure 11).

History– Fairlingtonia thyrsopteroides was originally described as a fern in the genus *Sphenopteris* by Fontaine (Fontaine, 1889) from the "Fish Hut above Dutch Gap Canal," and "Fredericksburg" localities; however the only remaining figured specimen was collected from the first locality (Fontaine, 1889). Berry (1911) transferred the species to *Ruffordia goeppertii* (Dunker) Seward and noted that the material identified as *Sphenopteris pachyphylla* and *S. spatulata* is identical to that of *S. thyrsopteroides.* The figured specimens of *S. pachyphylla* and *S. spatulata* were collected from "Entrance to Trent's Reach" (Fontaine, 1889). *Thyrsopteris pachyphylla* Fontaine from the "roadside near Potomac Run" near Lorton, VA also conforms to this species (Fontaine, 1889).

Etymology–The new generic name *Fairlingtonia* comes from the neighborhood of Fairlington, Virginia, U.S.A. where many well preserved specimens were collected by R. W. Brown in 1944.

Occurrences– Intersection of Covington and E. Clement Streets, Baltimore, Maryland, USA; Fish Hut above Dutch Gap (Fontaine, 1889); Entrance to Trent's Reach (Fontaine, 1889); "Road Side near Potomac Run," near Lorton, VA (Fontaine, 1889); USGS loc. 9030, Hillside along Highway I-395, south side of Four Mile Run,

Fairlington, Virginia, USA; LJH and JAD loc. 71-117, base of the bluff at Dutch Gap Canal in Henrico County, Virginia, USA. N37.375° W-79.359° (WGS84). Fontaine (Fontaine, 1889) also stated that "*Sphenopteris*" *thyrsopteroides* occurs in the collection from Fredericksburg, Virginia, but these specimens were not figured and are apparently lost. One specimen (Figure 8) lacks information about where it was collected, but the matrix is similar to other fossils from Fredericksburg. This may be the lost specimen.

Stratigraphic position and Age–lower part of the Potomac Group (Patuxent Formation equivalent) and Arundel Clay, Zone I. Aptian-earliest Albian, Early Cretaceous.

Description–F. thyrsopteroides plants were small, herbaceous, stoloniferous, and much-branched. The young stems were flexuous, but the older stems appear generally straight and more robust. Attached branches and buds occur in the axils of leaves. Fibrous adventitious root systems are occasionally attached to the stems in pairs at nodes. The leaves comprise a deeply dissected blade, marginal petiole, and decurrent, clasping leaf base without stipules. The leaves are helically arranged (alternate) along the stem. The petioles are short (≤5mm) and the leaf blade is small (leptophyll). The organization of the dissected leaf blade is variable; some leaves are best described as simple and twice pinnately lobed, whereas others are best described as palmately compound (trifoliate) with pinnately lobed leaflets. The size of the lobes and depth of the sinuses decreases smoothly toward the apex. The secondary lobes are alternate and anadromous. The ratio of laminar length to width is 1-1.25:1; the overall shape is ovate, but the lobes are obovate. The apex is obtuse and rounded; and the

base is obtuse and concave to decurrent. The insertion of the petiole to the blade is often asymmetrical. The primary venation is pinnate or palmate with three primary veins, but the characterization of the primary vein framework is related to the interpretation of the leaves as either compound or simple and lobed. The major secondary veins are craspedodromous; secondary vein spacing decreases distally and the secondary vein angle smoothly decreases proximally. The minor secondary veins are craspedodromous. A perimarginal vein is visible in the distal parts of the lobes. The tertiary vein framework is irregular reticulate, forming irregular areoles without freely ending veinlets. The glandular teeth at the apices of lobes have papillate structures that probably represent hydathodes and are vascularized by a medial principal vein that terminates at the apex of the tooth and thickened lateral accessory veins continuous with the perimarginal vein. Measurements of petiole width and leaf area on seven complete or nearly complete leaves yielded a mean PW^2/A value of 0.0203 and a corresponding average LMA of 74.5g/mm^2 +/- 4.8 using the equation of Royer et al. (Royer et al., 2010) for angiosperm herbs.

Discussion

Autecology

Fairlingtonia thyrsopteroides occurs in at least eight different collections from eight sites in Zone I of the Potomac Group in Maryland and Virginia, U.S.A. These collections come from mudstones and siltstones with little or no lamination (Upchurch and Doyle, 1981). The fine grained beds in which the plant fossils occur often alternate with poorly sorted, cross-laminated, coarse-grained beds. This pattern of sedimentation indicates rapid, near-channel preservation in overbank fines

associated with crevasse-splay deposits (Hickey and Doyle, 1977). Furthermore, the frequent preservation of leaves attached to slender stems—and in at least two cases the preservation of fine, branched, adventitious roots attached to a stem—suggests minimal transport prior to deposition. Together, this sedimentological information indicates that the fossils are nearly autochthonous (Wing, 1988); and that *F. thyrsopteroides* was a widespread plant that inhabited disturbance-prone near-channel riparian habitats.

The slender and flexuous stems of *Fairlingtonia* show that it was an herbaceous plant (Figs 4, 5, 11). The presence of lobed leaves with glandular teeth and short marginal petioles, rather than cordate, peltate, or filiform leaves with long petioles and entire margins, support the conclusion that *Fairlingtonia* was a terrestrial herb rather than an aquatic one (Stevens, 1956; Barral et al., 2013). Furthermore, the small size, presence of adventitious roots (Fig 10), and the abundance of resting buds in well preserved specimens (Figure 7) suggests a potential for vigorous opportunistic growth that is typical of creeping or scrambling herbs adapted to colonizing freshly disturbed substrates (Bellingham and Sparrow, 2000; Klimešová and Klimeš, 2003, 2007).

Characteristics of the petiole and leaf blade indicate that *Fairlingtonia* was able to photosynthesize under bright conditions. Whereas long petioles that hold the leaf blade up away from the ground are common among terrestrial forbs that compete for light in shady or densely vegetated habitats, short petioles and small leaves are more common in herbs that colonize freshly disturbed substrates where competition for light is not a factor (Givnish, 1982). *Fairlingtonia* has very short petioles, small

leaves, and likely had green stems. Lobed leaves are generally associated with adaptation to shade (Givnish, 1987); however, in very small leaves lobes are associated with high density of major veins, which promoted the maintenance of equable water potential across the leaf and high leaf hydraulic conductance (Sack et al., 2012; Sommerville et al., 2012). Small dissected leaves also enable rapid convective cooling, protecting the leaves from overheating under conditions of high light and still air (Schuepp, 1993; Feild et al., 2005; Sack and Holbrook, 2006; Sack et al., 2012). Thus, the combination of short petioles and small, dissected leaves in *Fairlingtonia* would have enabled rapid growth on bright, fresh substrates.

Another clue to the growth strategy and light environment of *Fairlingtonia* comes from the estimate of leaf mass per area (LMA). Plants with rapid resource acquisition typically have high mass-based photosynthetic and respiration rates, short leaf lifespans, fast growth rates, and low LMA, whereas plants with slower resource acquisition typically have low mass-based photosynthetic rate, longer leaf lifespans, slow growth rates, and high LMA (Westoby et al., 2002; Wright et al., 2004; Royer et al., 2010). Although LMA cannot be directly measured from leaf compression fossils, Royer et al. (2007, 2010) showed that LMA area can be estimated using a power law relationship between petiole width and leaf area ($PW^2/A \propto LMA$), both of which can be measured in fossils. Low PW^2/A values correspond with low LMA values. The inferred LMA of *Fairlingtonia* of 74.5g/mm^2 is a value typical of plants in riparian habitats (Royer et al., 2010).

Glandular chloranthoid teeth such as those observed in *Fairlingtonia* (Figs. 6, 7, 11) are common among plants that grow in wet soils and periodically experience

high humidity. Teeth of this type are sites of guttation; the loss of water at tooth apices prevents flooding of the leaf mesophyll under conditions of high soil moisture, high humidity, and low evaporative demand (Feild et al., 2005, 2009; Feild and Arens, 2007). Environments such as forest understories or riparian corridors in tropical and temperate climates typically host plants with chloranthoid teeth (Wolfe, 1971, 1979; Baker-Brosh and Peet, 1997; Wilf, 1997; Burnham et al., 2001; Kowalski, 2002; Kowalski and Dilcher, 2003; Feild et al., 2005); however, glandular chloranthoid teeth also occur in some aquatic or marginally aquatic ranunculalean herbs that grow under bright conditions (Stevens, 1956). The combination of the herbaceous habit and glandular teeth, in light of the features discussed above, indicates that *Fairlingtonia* was adapted to wet substrates but could photosynthesize effectively under bright conditions.

The distribution, sedimentological context, and morphology of the fossils provide strong evidence that *Fairlingtonia* was a widespread fast-growing herb that colonized bright, wet, riparian habitats in subtropical eastern North America during the Aptian-earliest Albian (approximately 125-109 million years ago). In the context of this study, the key difference between the riparian weed model and the ancestral xerophobia model is the predicted light environment of early angiosperms. The morphological and depositional evidence suggest that the ecology of *Fairlingtonia* is more consistent with the riparian weed model.

Finally, *Fairlingtonia* is several million years older than the mid-Albian, when angiosperm macrofossils are much better represented in the fossil record. By then, the record includes locally abundant eudicot angiosperm species with relatively high vein

density for the Cretaceous (6-10 mm•mm^{-2}) (Hickey and Doyle, 1977; Crane et al., 1993; Feild et al., 2011). Paleobotanists have long noted that the oldest angiosperm fossils are generally small plants with small leaves (Vakhrameev, 1952; Samylina, 1968; Doyle and Hickey, 1976; Taylor and Hickey, 1996; Jud and Hickey, 2013) and that fossil angiosperm wood is exceedingly rare in the Lower Cretaceous (Peralta-Medina and Falcon-Lang, 2012). This appears to be a real ecological pattern, at least in depositional environments where fossils are preserved, with important evolutionary implications rather than the product of an incomplete or biased fossil record. A given area of vegetation can support more species (i.e. higher alpha diversity), when most of the individuals in the community are small (Aarssen et al., 2006), which would likely have been as true in the Early Cretaceous as it is today. Furthermore, small herbs tend to have early reproduction, short generation times, high nucleotide substitution rates, and high net diversification rates compared to their woody counterparts (Dodd et al., 1999; Verdú, 2002; Smith and Donoghue, 2008). Therefore, small size may have been a key trait allowing early angiosperms to spread and diversify in Early Cretaceous communities dominated by gymnosperms and ferns even before derived vessel morphology, high vein density, and hydraulically optimized leaves permitted locally abundant angiosperms in the mid-Albian to Late Cretaceous and ultimately angiosperm-dominated ecosystems in the Late Cretaceous and Cenozoic.

Comparison with extant and fossil plants

Living seed plants are united by a suite of reproductive synapomorphies, but one of the most obvious synapomorphies is a vegetative character: axillary branching (Nixon et al., 1994; Mathews, 2009). *Fairlingtonia thyrsopteroides* can be confidently assigned to the seed plant clade based on the preservation of attached leaves that subtend branches (Figures 3, 9) and on the preservation of resting buds in the axils of leaves (Fig. 7). Four other vegetative characters together indicate *Fairlingtonia* is an angiosperm: (1) herbaceous habit, (2) hierarchical reticulate venation (3) glandular (chloranthoid) teeth, and (4) complex leaf dissection (Jud and Hickey, 2013). The combination of the herbaceous habit and hierarchical reticulate leaf venation is a rare condition among gymnosperms, but common in angiosperms (Hickey and Wolfe, 1975). Within crown group angiosperms, the terrestrial herbaceous habit is more common among eudicot and monocot angiosperms than in the ANA grade; however, given the disparity of plant habits among living ANA-grade angiosperms; the herbaceous habit may also have been common among ANA-grade angiosperms during the Early Cretaceous.

Evidence is mounting that either complex leaves are a synapomorphy of crown-group eudicots, or that the capacity to explore leaf morphospace is somehow enhances among eudicots (Doyle, 2007; Geeta et al., 2012; Barral et al., 2013; Jud and Hickey, 2013). However, lobed and compound leaves also occur outside of the eudicot clade in Cabombaceae, Laurales, Piperales, and monocots (Jud and Hickey, 2013). Specifically, the trifoliate-lobed to twice pinnate shape with rounded sinuses of *Fairlingtonia's* complex leaves is suggestive of a close relationship to eudicot

angiosperms. However, the arrangement of secondary lobes in *Fairlingtonia* is not typical of living eudicot angiosperms. The fronds of ferns that are twice (or more) cut may be described as anadromous, catadromous, or opposite depending on whether the first and most proximal pinnules occur along the acroscopic or basiscopic side of the pinnae (these terms may also be applied to the organization of the veins) (Milde, 1867). These alternate character states reflect the different ways in which the marginal blastozone of the leaf primordium is dissected and the establishment of auxin maxima at the teeth or lobe apices (Heidenhain, 1932; Gleissberg and Kadereit, 1999). To borrow these terms from pteridology and apply them to the analogous leaves of angiosperms, among the diversity of eudicots that I have examined that are palmately and pinnately lobed, or twice (or more) pinnately lobed, only some members of the basal eudicot family Proteaceae, and rarely some Asteraceae (e.g. *Bidens*) could be described as anadromous, whereas most leaves are catadromous.

The broad petiole bases in *Fairlingtonia* indicate that the petioles were at least partially clasping the stem (Figs. 5, 11), and the dark lines along the stem in figure 11 are suggestive of a lower leaf zone that forms a sheath nearly encircling the stem. In other specimens a leaf sheath is not visible (Figs. 7, 9). Sheathing leaf bases are normally associated with monocots rather than eudicots (Canales et al., 2005; Gunawardena and Dengler, 2006), but the lateral incorporation of cells from the shoot apical meristem into the bases of leaf primordia resulting in a clasping or sheathing lower leaf zone occurs in many seed plants (Rudall and Buzgo, 2002). In some herbaceous monocots (e.g. *Philodendron*) and in some eudicots (e.g. *Caltha,* Ranunculaceae), the lower leaf zone forms a sheath that fully encircles the shoot apex

(Stevens, 1956), but as the shoot apex grows beyond the protection of the leaf sheath the lateral portions of the sheath die and fall away, leaving a petiole that only partially clasps the stem. This process could explain the presence of the sheath in some specimens of *F. thyrsopteroides* (presumably those buried just after leaf expansion) and its absence in other, presumably more mature specimens, where buds and branches are visible in the axils of leaves (Figure 7, 9). I consider this interpretation tentative, with additional fossils needed.

Fairlingtonia is not the first Early Cretaceous angiosperm to be described with small dissected leaves, glandular teeth, and herbaceous stems. *Achaenocarpites capitellatus* Krassilov et Volynets from the mid-Albian of eastern Russian (Krassilov and Volynets, 2008) and *Sagaria clientana* Bravi, Lumaga, et Mickle from the mid-Albian of Italy (Bravi et al., 2010) are well understood species similar to *Fairlingtonia*. Whereas the leaves of *Fairlingtonia* are up to 1 cm long and have acropetal dissection, the leaves of *Achaenocarpites* are clearly trifoliate with intermediate basipetal pedate-acropetal dissection *sensu* Gleissberg and Kadereit (Krassilov and Volynets, 2008) and they range in size up to 10-16mm long. The leaves of *Sagaria* are fragmentary, but also appear to be >10mm long and are pinnately lobed. The largest lobes in *Sagaria* leaves occur midway between the base and apex of the leaf, which is consistent with the divergent class of leaf dissection. This level of variation in leaf dissection is typical across genera among living Ranunculales (Gleissberg and Kadereit, 1999). The reproductive structures of both *Achaenocarpites* and *Sagaria* indicate affinities with Ranunculalean eudicots.

Several other Early Cretaceous plants with complex dissected leaves and a probable herbaceous habit are known as well, including *Vitiphyllum multifidum* (Fontaine, 1889), *Vitiphyllum* sp. (Huang and Dilcher, 1994) *Ceratophytum schornii* (Boyd, 1998), *Archaefructus liaoningensis* (Sun et al., 1998), *A. sinensis* (Sun et al., 2002), *A. eoflora* (Qiang et al., 2004), *Ternaricarpites floribundus* (Krassilov and Volynets, 2008), *Leefructus mirus* (Sun et al., 2011), *Iterophyllum lobatum* (Barral et al., 2013), and *Potomacapnos apeleutheron* (Jud and Hickey, 2013). In each of these cases, with the possible exception of *Archaefructus*, the fossils were thought to be more closely related to eudicots than any other group of angiosperms. There are also herbaceous angiosperm fossils from the Aptian that are thought to be more closely related to other groups, such as the chloranthalean plant from the Koonwarra formation of Australia (Taylor and Hickey, 1990), *Acaciaephyllum* (monocot) from the Potomac Group (Doyle et al., 2008), and *Pluricarpellatia* (Nymphaeales) from the Crato Formation in Brazil (Mohr et al., 2008), but these generally have simple leaves. Together, the growing number of Barremian(?), Aptian, and Albian herbaceous angiosperms suggests that such crown-group angiosperms (perhaps mostly eudicots and stem-eudicots) were diverse and widely distributed at low and mid-latitudes during the Early Cretaceous.

Based on the mode of leaf dissection, the herbaceous habit, and the attachment of the leaves to the stem, and the glandular chloranthoid teeth, I conclude that *Fairlingtonia* most likely belongs nested among Ranunculales and Proteales, or along the branch leading to crown group eudicots. New collections including associated fruits, flowers, or pollen of *F. thyrsopteroides* could provide the additional characters

necessary to determine its phylogenetic position with more confidence. Nevertheless, using existing characters, I conclude *Fairlingtonia* is nested within crown-group angiosperms above the ANA-grade that strongly influenced the ancestral xerophobia model of early angiosperm ecology.

Feild et al. (2004) proposed that the humid, shady understory favored the evolution of hierarchical reticulate venation and vessels in the earliest angiosperms, and also paved the way for cooption and modification of these traits in variety of habitats with higher evaporative demand (i.e. bright or dry conditions). Thus, *Fairlingtonia* appears to be consistent with both the riparian weed and the ancestral xerophobia models. On the other hand, if future research demonstrates that *Fairlingtonia* or similar fossil plants in fact belong deeper in angiosperm phylogeny, the inferred ancestral habit of angiosperms would be significantly altered, contradicting the ancestral xerophobia hypotheses. This possibility that the morphological and ecological diversity of extinct basal angiosperms was broader than what remains among the living representatives of ANA-grade angiosperms, remains open given the range of ecological traits found in living *Amborella*+Austrobaileyales and Nymphaeales.

Conclusions

- A suite of vegetative characteristics demonstrate that *Fairlingtonia thyrsopteroides* is not a fern, but instead an early herbaceous angiosperm.
- *F. thyrsopteroides* is the most complete angiosperm species from the lower part of the Potomac Group (Zone I, Aptian-earliest Albian).

- *F. thyrsopteroides* was an herbaceous colonizer of bright, disturbed habitats along the humid riparian corridors of eastern North America during the Early Cretaceous; it was a riparian weed.
- The reinterpretation of *F. thyrsopteroides* does not provide grounds to reject the ancestral xerophobia hypotheses in favor of the riparian weed hypothesis. Instead, these hypotheses may apply to different parts of the angiosperm phylogeny and different aspects of early angiosperm paleoecology.
- Based on current fossil evidence it appears that early angiosperms were generally small plants and rare components of plant communities, but they were diverse and widespread across low and mid-latitudes during the Aptian and early Albian.
- Small size and vigorous vegetative growth were common features of angiosperms, or perhaps eudicot angiosperms in particular, during the early phase of their diversification roughly 125-110 Million years ago, before angiosperms began to dominate local communities in the mid and Late Cretaceous, and ultimately most of the world during the Late Cretaceous and Cenozoic.

Tables and Figures

Figure 1. Map of Lower Cretaceous Potomac Group outcrop in Virginia and Maryland, USA. Note the sites from which the fossil specimens described here were collected. (1) Entrance to Trent's Reach, (2) Banks of Dutch Gap Canal (3) base of the bluff at Dutch Gap (LJH JAD 71-117), (4) Fish Hut above Dutch Gap, (5) Fredericksburg, Virginia, (6) roadside near Potomac Run; near Lorton, Virginia. (7) Fairlington, Virginia (USGS 9030), (8) South of Federal Hill Park in Baltimore, MD.

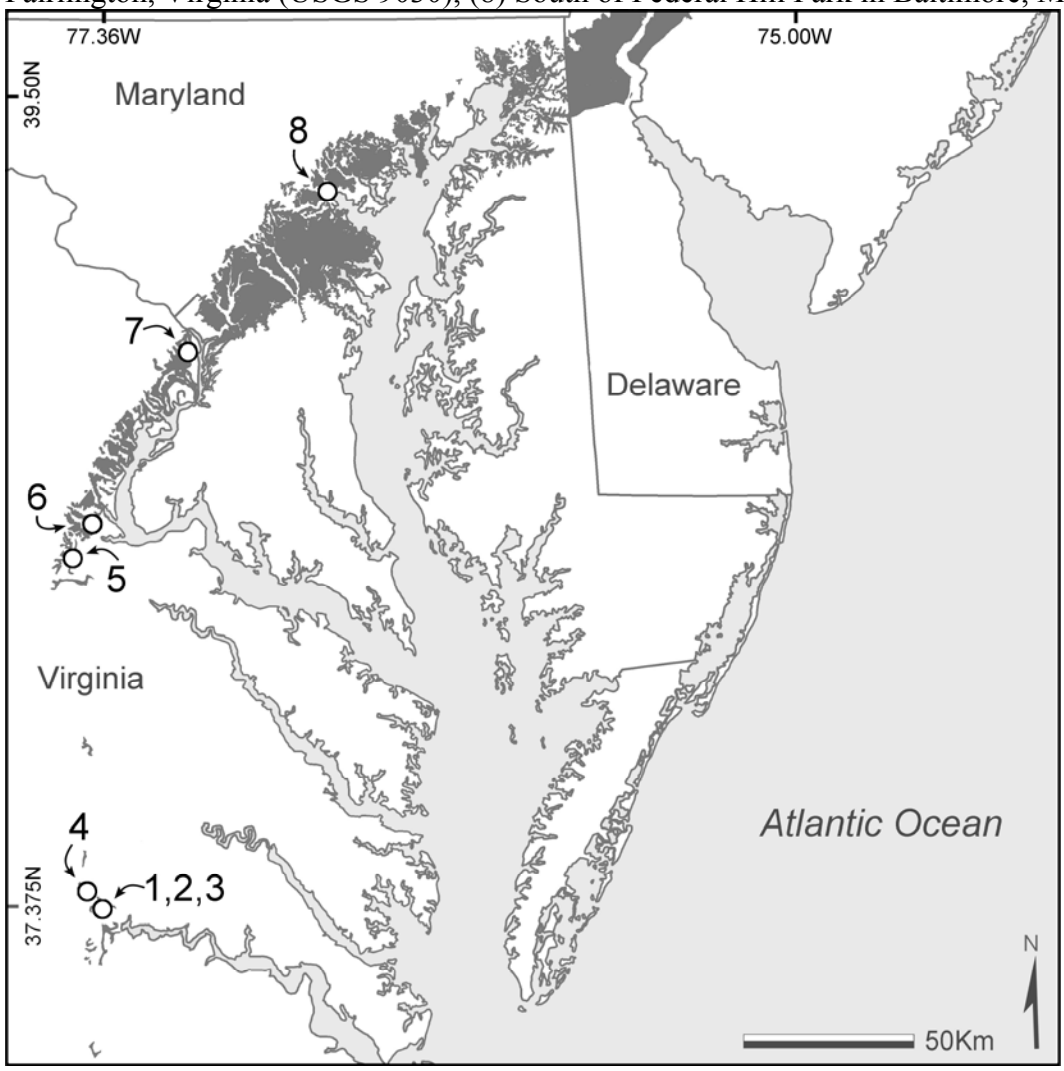


Figure 2. Age of the lower part of the Potomac Group modified from Doyle et al. (1992) and Hochuli et al. (2006). The dates on the left are from Gradstein et al. (2012). Some of the sites where the fossils described here were collected are in the lower part of Zone I and some are in the upper part of Zone I.

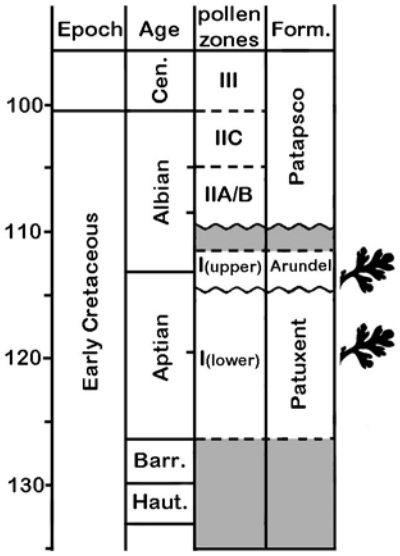


Figure 3. Holotype. USNM Specimen 597566 from "Fish Hut above Dutch Gap." *Fairlingtonia thyrsopteroides* comb nov. Note the leaf subtending the leafy lateral branch at arrow. **Figure 4.** USNM Specimen 597567. Originally described as "*Sphenopteris" pachyphylla* Fontaine from "Trent's Reach." Note the lobed leaves attached to a flexuose stem. **Figure 5.** USNM Specimen 597568. Originally identified as "*Sphenopteris" thyrsopteroides*. Locality uncertain. Note the lobed leaves attached to a flexuose stem. **Figure 6.** USNM Specimen 597569. Originally identified as *Thyrsopteris pachyphylla* from "Station near Lorton, VA." This is the largest leaf that I identified that conforms to *Fairlingtonia thyrsopteroides*.

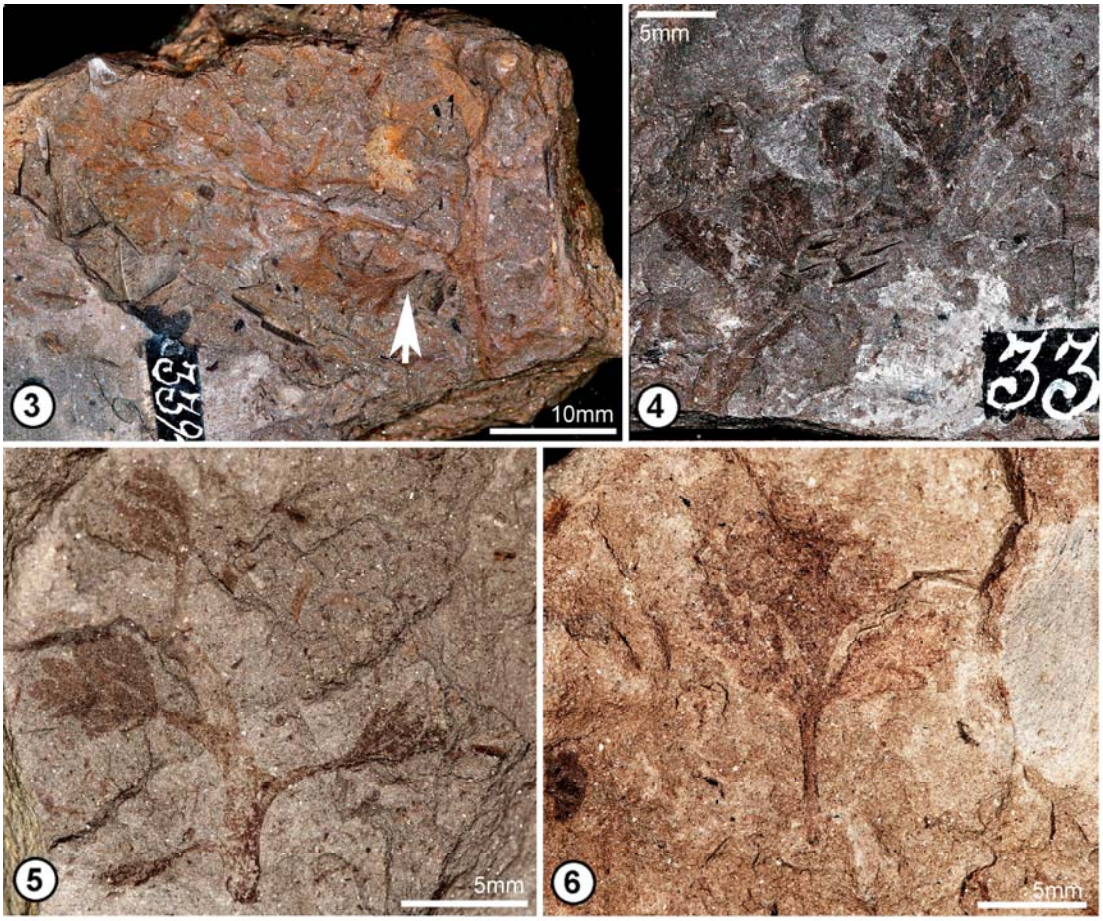


Figure 7. USNM Specimen 597570 from USGS loc. 9030 (Fairlington, VA) showing lobed leaves attached to a stem with a bud in the axil of a leaf at white arrow. **Figure 8.** USNM Specimen 597571 from either Fredericksburg, VA or "Fish Hut above Dutch Gap" based on the lithology. Note the variation in leaf morphology between rather symmetrical leaves (right arrow) and asymmetrical leaves (left arrow). **Figure 9.** USNM Specimen 597572 (WCB Specimen 5975) from Covington and Clemet streets, just south of Federal Hill Park in Baltimore, MD. Note branches with subtending leaves at arrow.

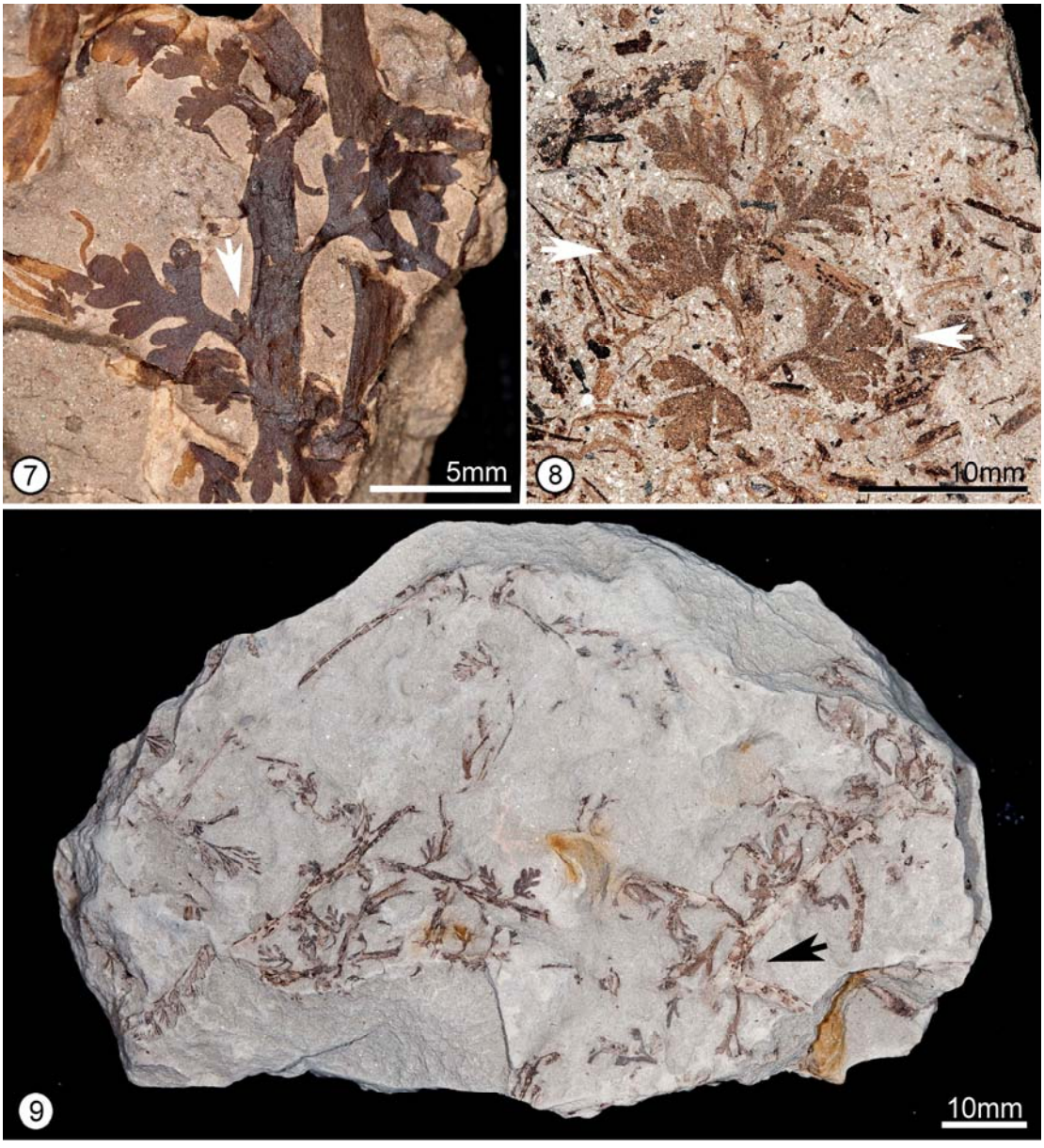
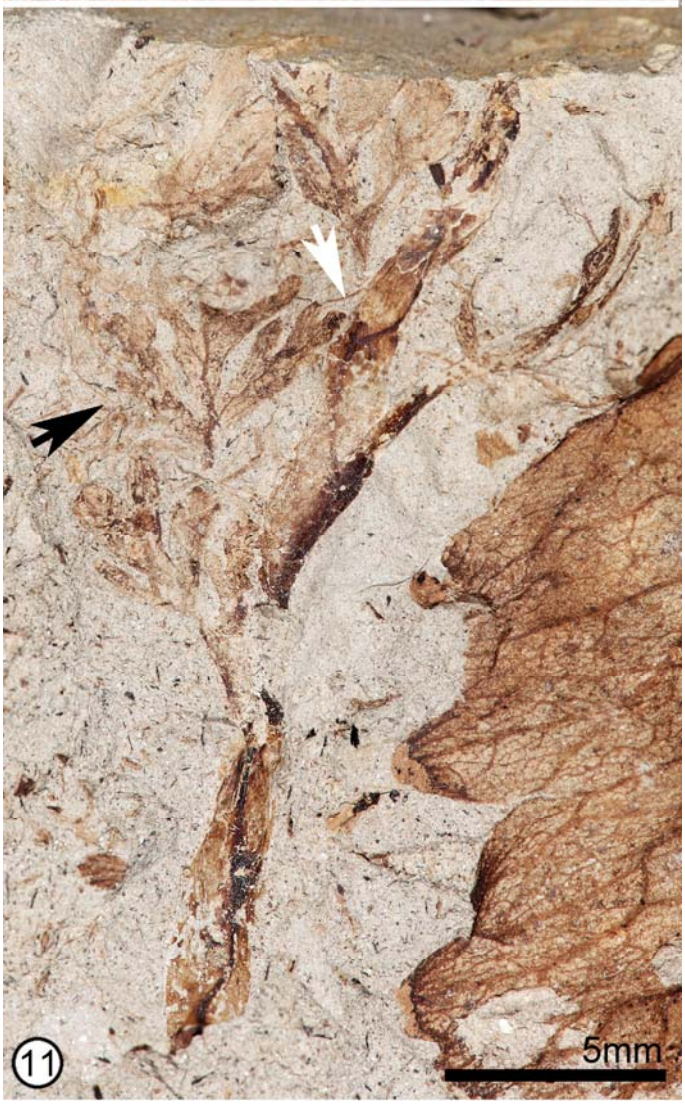


Figure 10. USNM Specimen 597573 from “Fish Hut above Dutch Gap.” Note the pair of fibrous adventitious roots attached to the stem at arrow. **Figure 11.** Composite image of YPM Specimens 60054a and 60054b. Note the poorly organized venation of the leaf (black arrow), and the axillary bud adpressed to the stem (white arrow). Also note the sheathing leaf bases along the stem indicated by dark, curving lines that meet at nodes (6x).


10
5mm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Chapter 4: Large scale patterns in the distribution of angiosperm diversity based on Lower Cretaceous plant megafossil collections from the United States

Abstract

Collections of plant macrofossils from the Lower Cretaceous of the United States document plant community change during the early diversification of angiosperms. These data were compiled from my own examination of museum collections and from literature sources. The pre-Albian Early Cretaceous is poorly sampled in the United States, but fossil-bearing deposits are known from across western North America. Angiosperm megafossils first occur in Aptian-earliest Albian deposits. The distribution of angiosperm megafossils in Albian deposits indicates a broad environmental spread among angiosperms collectively. Angiosperms were uniformly rare components of many plant communities for much of the Early Cretaceous, becoming locally abundant only in the middle to late Albian. Despite evidence for a high diversification rate among angiosperm, observed species richness within plant megafossil collections does not increase through the Lower Cretaceous. This pattern parallels that found in the palynomorph record, and contrasts with the signal of increasing species richness through the Cretaceous obtained by earlier workers who compiled species lists for whole floras. This suggests that the angiosperm diversity was manifested over edaphic and climatic gradients during the Early Cretaceous, rather than by higher local richness.

Introduction

The fossil record of flowering plants (angiosperms) and insights from molecular phylogenetic studies provide strong evidence that the diversification of crown-group angiosperms began during the Early Cretaceous (Doyle, 2012; Magallón et al., 2013). Our understanding of how angiosperm diversity was incorporated into plant communities remains rudimentary; however, the absence of a mass extinction event prior to the diversification of angiosperms implies that intrinsic features of angiosperms enabled them to diversify despite the presence of incumbent groups. This could have proceeded through the displacement of non-angiosperm species (Knoll, 1986), or through the exploitation of ecological opportunities that were unavailable to other plants groups, thus augmenting diversity (Niklas et al., 1985).

Fossil leaf assemblages provide good estimates of local diversity through time for several reasons. First, the complex vein networks of leaves provide high taxonomic precision, and morphotypes correspond closely to biological species (Johnson, 1989). Second, studies of modern leaf litter and recent deposits indicate that most parautochthonous to autochthonous leaf assemblages are buried rapidly during flood events and therefore represent ‘snapshots’ of plant communities with minimal time averaging, preserving relative abundance and co-occurrence information (Gastaldo, 1988; Burnham et al., 1992; Burnham, 1994; Wing and DiMichele, 1995). Third, because dispersed leaves do not survive transport well, sedimentary features associated with collections of well-preserved leaves generally reflect local and regional environmental conditions that are relevant to understanding

the biology of the plants from a particular site (Greenwood, 1991; Davies-Vollum and Wing, 1998).

Here I examine the diversity of Early Cretaceous plant communities by tabulating and analyzing collections of leaf megafossils from parautochthonous assemblages. I compiled this dataset from the published literature and from my own inventory of the collections housed in the Dept. of Paleobiology at the Smithsonian National Museum of Natural History in Washington D.C., USA. I have operationalized alpha diversity as the informal taxon (morphotype) richness at a given site, which is usually represented by a single collection of fossils. I did not develop a comprehensive taxonomic classification of plant fossils between sites because of time constraints. I limited the analysis to the Lower Cretaceous deposits of the contiguous United States. With these data I test two hypotheses: 1) On average, alpha diversity increased as flowering plants diversified during the Early Cretaceous, and 2) Early angiosperm diversity and dominance were initially restricted to a subset of available environments, particularly disturbance-prone riparian habitats (Hickey and Doyle, 1977). I also review the literature on angiosperm paleoecology to evaluate the evidence for changes in spatial patterns of diversity at larger spatial scales.

Previous studies have indicated that angiosperm abundance and diversity were decoupled during their early diversification (Wing et al., 1993; Lupia et al., 1999). By grouping collections based on relative abundance information I can determine if the Lower Cretaceous leaf record provides support for a macroevolutionary lag between the diversification of angiosperms and their increase in abundance (Jablonski and Bottjer, 1990; Jackson and Erwin, 2006).

Methods

Sample Size

Estimates of biological diversity are strongly affected by the number of individuals observed (sample size) and the relative abundance of species in an assemblage community (Magurran, 2004). Collections of fossil plants are often non-random subsets of the specimens encountered in the field depending on the goals of the collectors, such as obtaining well-preserved specimens or simply documenting species presence. Metadata on sample size and relative abundance are usually lacking. Fortunately, the size of the original sample from which a historical plant fossil collection was drawn can be roughly estimated using site descriptions and by counting the number of rocks in museum collections. I scored each collection in this dataset using a semi-quantitative scale ranging from 1 to 3 based on my estimate of the total number of plant fossils that must have been observed by the collector(s) at the site where the collection was made (original sample size). I estimated the original sample sizes based on the number of specimens in museum collections and on descriptions of the collecting sites from field notes and publications. A score of "1" means that most likely that fewer than 50 identifiable plant fossils were observed in the field or that the collection is very small and there is no way to confidently estimate the original number of fossils observed in the field, "2" means that likely between 50 and 300 identifiable plant fossils were observed in the field, and "3" means that >300 identifiable plant fossils were encountered in the field. I used all collections for analyses of dominance patterns, but I used the subset of collections scored as "2" or "3" for analyses of alpha diversity through time. This approach

retains information from well-sampled, low-diversity collections. Previous studies of diversity in Early Cretaceous plants excluded low diversity collections under the assumption that low diversity was caused by low sampling effort (Lidgard and Crane, 1988), a procedure that eliminates good samples of low diversity vegetation.

Diversity

Historical museum collections are an invaluable source of paleoecological information (Allmon, 2005), but counts of the relative abundance of species within museum collections are not necessarily reliable and raw data on relative abundance of species and sampling effort are rarely preserved with the collection. A simple method of estimating relative abundance was developed by Harnik, who proposed using the abundance distributions in new bulk samples to assign maximum proportional abundance values to rare "list only" species that are not present in the bulk sample but are present in museum collections from the same site (Harnik, 2009). Plant megafossils are generally not sampled in bulk the same way that mollusks and other "small shelly fauna" are, but I developed an analogous approach. The fossiliferous rocks that comprise historical leaf megafossil collections often bear multiple identifiable fossils if the density of fossils in the matrix is high. It is often clear that only one of the fossil specimens was of interest when the rock was collected. The relative abundances of the species represented in the collection as a whole can be estimated by counting the number of times each morphotype occurs, excepting those occurrences where it was clearly the "specimen of interest." The identity of the most common species can then be determined, and the maximum proportional abundance

of the specimens that do not occur in the collection other than as a "specimen of interest" can be estimated.

Using the approach above, I identified the most abundant morphotype in each collection wherever possible and then assigned it to the most precise taxonomic group possible. However, some historical collections had such even abundance distributions, and the descriptions of collecting effort and sites were so vague or problematic, that I could not identify the most common morphotype. Because a comprehensive taxonomic revision of all the species in all of the collections in this study was beyond the scope of this work, I compiled summary information on the diversity and abundance structure of the remaining morphotypes in each collection. I counted the number of distinct foliar morphotypes, I identified the most common morphotype in each collection and I scored each collection based on the abundance of angiosperm species using a semi-quantitative scale with scores ranging from 0 - 2. A score of "0" means that no angiosperm morphotypes occur in the collection, a score of "1" means that some rare or common angiosperm morphotypes are present but the collection is dominated by a non-angiosperm morphotype, and a score of "2" means that the most common morphotype in the collection is an angiosperm.

One drawback of this approach is that I did not consider the relative abundance of angiosperms, ferns, conifers, and other gymnosperm specimens independent of species identity. Such an approach would have the advantage of considering a flora angiosperm-dominated if the assemblage includes many common angiosperm morphotypes, but the single most common morphotype is a fern or gymnosperm (i.e. assemblages that have high evenness and are angiosperm-rich). An

analysis of this type might provide a slightly different estimate of when angiosperm-dominated floras first appeared and subsequently how common they were, but it would also require more reliable estimates of species abundance than is often available from historical museum collections.

Previous studies have indicated that angiosperm abundance and diversity were decoupled during their early diversification (Wing et al., 1993; Lupia et al., 1999). By grouping collections based on relative abundance information I can determine whether the Lower Cretaceous leaf record provides support for a macroevolutionary lag between the diversification of angiosperms and their increase in abundance (Jablonski and Bottjer, 1990; Jackson and Erwin, 2006).

Environmental variables

The environmental details that I recorded included site location, age, formation, matrix grain size, matrix bedding, and matrix color. I estimated the age of each collection by reviewing recent geological literature concerning the Lower Cretaceous deposits, assigning absolute ages based on recent estimates provided by the International Commission on Stratigraphy (Gradstein et al., 2012). I then assigned every collection to one of four time bins: 145-125Ma, 125-115Ma, 115-105Ma, and 105-95Ma. I collected data on three lithological variables (grain size, color, and bedding) and used that information to score the collections as "high energy," "moderate energy," or "low energy." Collections scored as "high energy" are preserved in cross-bedded or cross-laminated sandstones. Collections scored as "moderate energy" are preserved in massive or ripple laminated siltstones.

Collections scores as “low energy” are preserved in mudstones or claystones that are either massive or flat laminated (Table 1).

Results

Four broad patterns characterize this dataset (Appendix V) and have important implications for interpretation of spatiotemporal patterns in plant diversity. First, older time periods are less well collected. Out of 229 total collections made over a century of work, 74% were assigned to time bins 3 and 4, the latest Aptian-early Cenomanian deposits (Figure 2). Second, most of the collections were made from low-energy deposits that are characterized by at least two of these three features: fine-grain size (clay-silt), flat lamination, and high organic carbon content (Figure 3). Third, about half of the collections in the dataset were scored as low sample size because the collection is likely based on few (<50) observations of fossils in the field (Figures 2 &3). The relationship between sample size and species richness is triangular (Figure 4). Small samples have low diversity, and large samples include species rich and species poor collections. These three patterns are the result of a combination of taphonomic and collector bias. Therefore, this dataset represents a highly non-random sample of Early Cretaceous plant communities. These attributes of the data suggest that caution is warranted in attempting to distinguish patterns that reflect real paleoecological patterns from those that are generated by sampling effects.

In North America the oldest unequivocal angiosperm fossils come from the Aptian-early Albian deposits of the Potomac Group in Maryland and Virginia (Doyle and Hickey, 1976; Hochuli et al., 2006). These fossils include evidence of ANA-grade angiosperms (Upchurch, 1984a), monocots (Doyle et al., 2008) and eudicot

angiosperms (Jud and Hickey, 2013). Roughly coeval deposits from the early-middle Albian portions of the Cloverly and Kootenai formations in Wyoming and Montana also include evidence of eudicot angiosperms (Figure 5). The collections that include these early angiosperms share probable eudicot species that had small, complex leaves and provide direct or indirect evidence of the herbaceous habit. They are also all preserved in low-energy fluvial mudstone beds deposited under a seasonal, subtropical to temperate climate (Upchurch and Doyle, 1981; Vuke, 1984; Ufnar et al., 2004; Elliott Jr. et al., 2007). The plants probably grew in wetland and pond-margin habitats that were periodically disturbed by sediment input from flooding.

Angiosperms were rare components of plant communities long before they dominated plant communities (Figure 6 & 7). Angiosperm fossils from the Aptian to middle Albian are represented by few specimens even in collections that were scored for moderate or large sample size. The paucity of large collections from pre-Albian deposits makes it difficult to determine if new collections will yield older rare angiosperm fossils, given that angiosperm fossils are known from Hauterivian-Barremian sites elsewhere in the world (Doyle et al., 1977; Hughes et al., 1991; Brenner, 1996; Schrank and Mahmoud, 2002; Zhang et al., 2014). The appearance of angiosperm-dominated local assemblages in fluvial depositional systems during the late Albian is probably a real ecological phenomenon, however, rather than a reflection of taphonomic or sampling, bias because abundant species are likely to be detected even when sample size is small.

Although angiosperm dominance is common among the late Albian and Cenomanian plant fossil assemblages included in this study, it is not ubiquitous.

Many assemblages are dominated by fern or conifer foliage. I predicted that angiosperm dominated assemblages would be more common in collections made from deposits in massive or ripple laminated sandy deposits; however, the "energy of deposition" categories defined in this study do not explain the observed distribution of angiosperm dominance (Table 3). In this dataset angiosperm megafossils are initially restricted to low-energy deposits, and by the late Albian-Cenomanian collections dominated by angiosperm megafossils occur in all three environmental categories.

The 115 sites with moderate or large sample size have an average of ~10 morphotypes per site, but the modal value is two morphotypes. Maximum collection richness increased from 18 to 35 from the Early to early Late Cretaceous. The four species-rich sites from the Cenomanian are based on much larger samples than almost all other sites; well over 1000 specimens were examined at each of these sites to obtain the richness values (Wolfe and Upchurch, 1987; Upchurch and Dilcher, 1990; Wang and Dilcher, 2006, 2009). Despite the increase in maximum richness through time in this dataset, the average richness of well-sampled collections is weakly correlated with age, and the average richness decreases slightly in younger samples (Figures 8). A permutation test of the hypothesis that alpha diversity increases with time shows that the data are consistent with the null hypothesis that richness is not related to age ($p=0.8$).

Discussion

Species Richness through Time

The mounting evidence for high diversification rates among angiosperms during the Early Cretaceous (Davies et al., 2004; Friis et al., 2010; Magallón et al., 2013), leads to the prediction that angiosperm-bearing collections should be more species rich than older, pre-angiosperm collections because they should include many angiosperm species. This prediction is not supported by the data presented here. This may represent a failure to detect a real increase in average species richness, or it may be that average local diversity really was stable through the Early Cretaceous in North America. Each of these interpretations has important implications.

If local species richness really was stable through the Early Cretaceous despite elevated diversification rates among early angiosperm lineages, then the increase in angiosperm diversity should be apparent at larger spatial scales. Palynological samples record plant diversity at a somewhat broader spatial scale than leaf megafossil collections. Generally, pollen samples represent hundreds of square meters to many hectares or square km of the surrounding vegetation (Jacobson Jr. and Bradshaw, 1981; Traverse, 2007), typically one or more orders of magnitude more area than leaf samples. Previous studies of Cretaceous pollen samples from North America and Australia show no significant increase in within-sample richness through the Cretaceous (Lupia et al., 1999; Nagalingum et al., 2002).

Previous analyses of plant diversity compared species richness at the larger spatial scales more appropriate for detecting change across large-scale edaphic, physiographic, and climatic gradients, as well as disturbance regimes (Knoll, 1986;

Lidgard and Crane, 1990). In these studies, the authors compiled species lists for entire formations or members into 'floras' and plotted the species richness of floras through time. The total species richness of entire geologic members or formations could be considered comparable to a time-averaged version of gamma diversity (Knoll 1986) because geologic formations span entire depositional basins, i.e. tens to thousands of square kilometers (10^6-10^{10} m^2). Therefore, an increase in the average species richness of whole floras could result from increasing alpha diversity or increasing beta diversity (Whittaker, 1960). Both studies of plant diversity through time found an increase in average species richness of floras through the Cretaceous, but no relationship between age and richness on a per-sample basis (this study; Lupia et al. 1999), the pattern found by Knoll et al. (1986) and by Crane and Lidgard (1990) could be interpreted as support for the hypothesis that angiosperm diversity was manifest at broad spatial scales across edaphic, physiographic, and disturbance gradients. However, these studies did not standardize samples ("floras") by number of specimens or number of sites.

There are several possible explanations for a failure to detect a real increase in average alpha diversity. First, it may be that the average richness of pre-angiosperm collections is overestimated in this dataset because well-sampled collections with very low richness are underrepresented in pre-Aptian deposits. This could be an important bias in this dataset if collectors typically stopped collecting early when an assemblage yielded only one or two morphotypes and no angiosperm fossils. If low diversity communities were the norm during the early part of the Early Cretaceous, then including additional well-sampled, low-diversity collections from pre-Aptian

deposits would increase the slope of the best fit line. Second, it could be the case that increasing alpha diversity during the Early Cretaceous is difficult to detect, even in large collections of leaf megafossils. This appears likely for two reasons. First, collections of well-preserved plant adpression fossils are highly local samples of biodiversity, generally drawn from vegetation growing in areas of a few square meters to a few thousand square meters (Greenwood, 1991; Burnham et al., 1992; Burnham, 1993). Therefore, collections of fossil leaves may often underrepresent alpha diversity because species richness is limited by the number of individual plants growing in a small area. Second, even if the highly local nature of leaf megafossil collections is not preventing the detection of increasing alpha diversity through time, there is other evidence to suggest that most angiosperm species were rare, small, herbaceous, insect-pollenated plants, and these are be difficult to detect simply because they are rare (Preston, 1964), and the preservation bias against plants that shed few leaves and pollen exacerbates the detection problem (Niklas and Enquist, 2001; Friedman and Barrett, 2009). A bias against detection of small, insect pollinated herbs in pollen and leaf assemblages is suggested by the abundance and diversity of angiosperms in some Aptian assemblages preserved as small particles of charcoalified plant matter, despite the absence or rarity of angiosperm fossils from nearby megafloras and pollen samples (Eriksson et al., 2000).

Early Angiosperm Habitats

Despite their rarity in Early Cretaceous fossil assemblages, angiosperms were widely distributed at low and middle latitudes by the Aptian. Evidence for this distribution comes from pollen, mesofossils, and macrofossils preserved in fine-

grained lacustrine and fluvial facies around the world (Doyle and Hickey, 1976; Friis et al., 1994; Mohr and Friis, 2000; Barale and Ouaja, 2001; Sun and Dilcher, 2002; Zhou et al., 2003; Coiffard et al., 2007; Archangelsky et al., 2009). Given this distribution, rare angiosperm megafossils may yet be found in the Barremian-Aptian deposits of western North America as well. The restriction of the earliest angiosperm megafossils to fine grained facies both in this dataset and abroad could reflect the suitability of these depositional environments for the preservation of small, flimsy, herbaceous plants, and/or an affinity of such plants for wet microsites in general (Feild et al., 2009).

By the middle Albian angiosperm fossils occur in collections from all three environmental categories recognized in this study, and by the late Albian to Cenomanian time interval angiosperm-dominated collections occur in all three environmental categories recognized in this study. However, angiosperm dominance is not ubiquitous even in the youngest time period considered. Many Albian-Cenomanian communities were dominated by ferns or conifers. Therefore, angiosperm dominance appears to be both delayed and patchy across Early Cretaceous landscapes, in contrast to angiosperm presence, which spread earlier and evenly.

I predicted that local angiosperm abundance would be correlated with environment of deposition because previous workers had concluded that early angiosperms were primarily weedy herbs and shrubs adapted to colonizing disturbance-prone channel-margin habitats (Hickey and Doyle, 1977). Under this hypothesis, angiosperm dominance should be most common in collections from

parautochthonous terrestrial deposits indicative of high-energy deposition. However, the distribution of angiosperm dominated sites was controlled by factors not captured by the general depositional categories used here. Other factors that might have complicated the distribution of angiosperm dominance include disturbance by fire and megafauna (Wing and Tiffney, 1987; Bond and Scott, 2010).

Conclusions

1) Alpha diversity of plants, as estimated from local megafossil and pollen samples, did not increase with the diversification of flowering plants during the Early Cretaceous. This is surprising because there is ample evidence based on fossil-calibrated molecular phylogenies for high diversification rates during the Early Cretaceous. There is good reason to suspect that the results are controlled primarily by sampling bias and taphonomic bias. The absence of an increase in alpha diversity could reflect either preservation biases against rare, small, insect-pollinated herbs, a common life-form among early angiosperms, or samples drawn from such small areas that they do not record changes in alpha diversity, however the latter should not be a problem if most early angiosperms were very small plants.
2) Although I did not test for an increase in beta diversity through time, the stability of alpha diversity through time and the apparent increase in angiosperm species richness through time suggests that increasing angiosperm diversity during the Early Cretaceous was at least partly manifested at the beta or landscape spatial scale. However future studies that explicitly standardize samples by specimens and sites are needed.

3) Angiosperms are consistently rare components of collections from Aptian-early Albian deposits despite evidence that they were diverse and geographically widespread. Angiosperm dominance appears to have lagged millions of years behind the initial diversification of the crown-group. The lag of more than 5Ma between the first occurrence of angiosperms in North America (Aptian) and the first occurrence of angiosperm-dominated megafossil collections (late-Albian) is real and may increase if rare, early angiosperm fossils are discovered in the future.
4) Collectively, early angiosperms appear to have occupied a wide variety of habitats at the local level, which is entirely consistent with the hypothesis that they were weedy plants with early reproduction and generalist pollination strategy.
5) During the mid Albian-Cenomanian angiosperm dominance was patchy, but high abundance is not correlated with the coarsely defined habitat categories recognized here. The absence of a correlation between angiosperm dominance and disturbed habitats in the Albian-Cenomanian is surprising because angiosperms of this age have been reconstructed as weedy riparian plants. The lack of correlation between angiosperm dominance and depositional environment could indicate broader habitat tolerances than previously thought, or the importance of disturbance events such as fire and megafaunal feeding that would not be reflected in sedimentological features.

Tables and Figures

Table 1. Lithological features used to classify collections into categories based on energy of deposition

Lithology		
Bedding	Grain size	Interpretation
flat laminated, massive	clay, mud, silt	low energy
cross laminated, ripple laminated	silt, vf sand	moderate energy
cross laminated, cross bedded, massive	f sand, sand	high energy

Table 2. Counts of sites showing the distribution of angiosperm fossils among depositional categories through time. During the Aptian angiosperms are restricted to low energy deposits. During the early and middle Albian angiosperm occur in all distributional categories but the distribution is biased toward low-energy deposits; the ages of the two angiosperm-dominated collections are poorly constrained and may be overestimated. During the late Albian and Cenomanian angiosperms are distributed evenly among categories, but angiosperm dominance is not ubiquitous.

125-115Ma	energy of deposition			
angiosperms	low	mod	High	total
absent	15	3	1	19
present	6	0	0	6
dominant	0	0	0	0
total collections	21	3	1	25

115-105Ma	energy of deposition			
angiosperms	low	mod	High	total
absent	15	12	2	29
present	6	3	1	10
dominant	0	2	0	2
total collections	21	17	3	41

105-95Ma	energy of deposition			
angiosperms	low	mod	High	total
absent	4	0	3	7
present	21	3	11	35
dominant	18	7	11	36
total collections	43	10	25	78

Figure 1. Map of Lower Cretaceous Plant Megafossil Collections from the United States

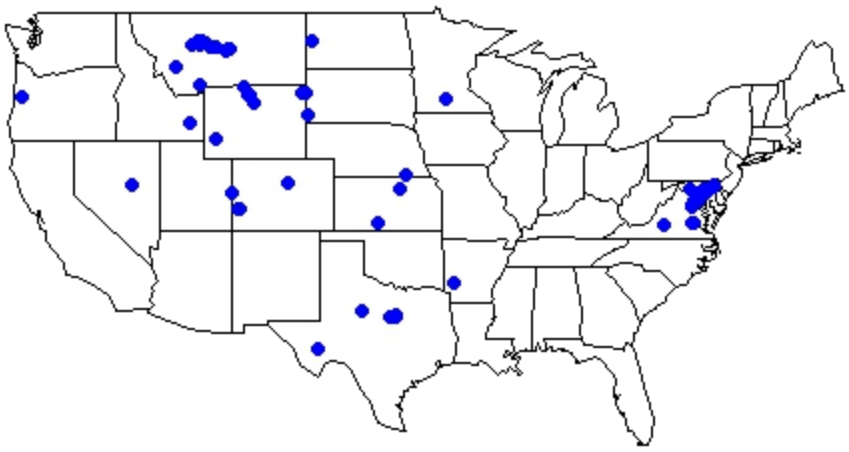


Figure 2. Distribution of plant megafossil collections by age. Lower Cretaceous plant megafossil collections were assigned to one of four Early Cretaceous time bins based on the median age estimate for each collection. In the United States the Berriasian-Aptian interval is poorly sampled for plant megafossils.

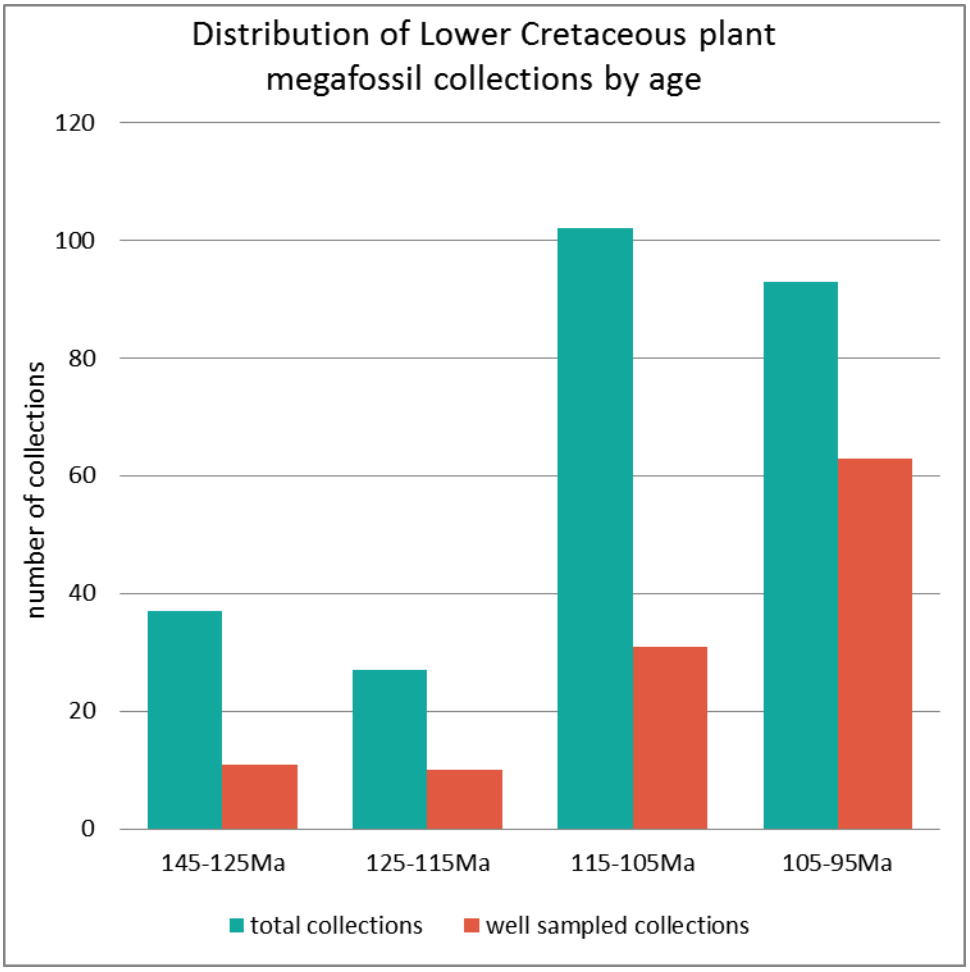


Figure 3. Plant megafossil collections grouped by energy of deposition. Categories are based on grain size and bedding features. Most collections are scored as low energy.

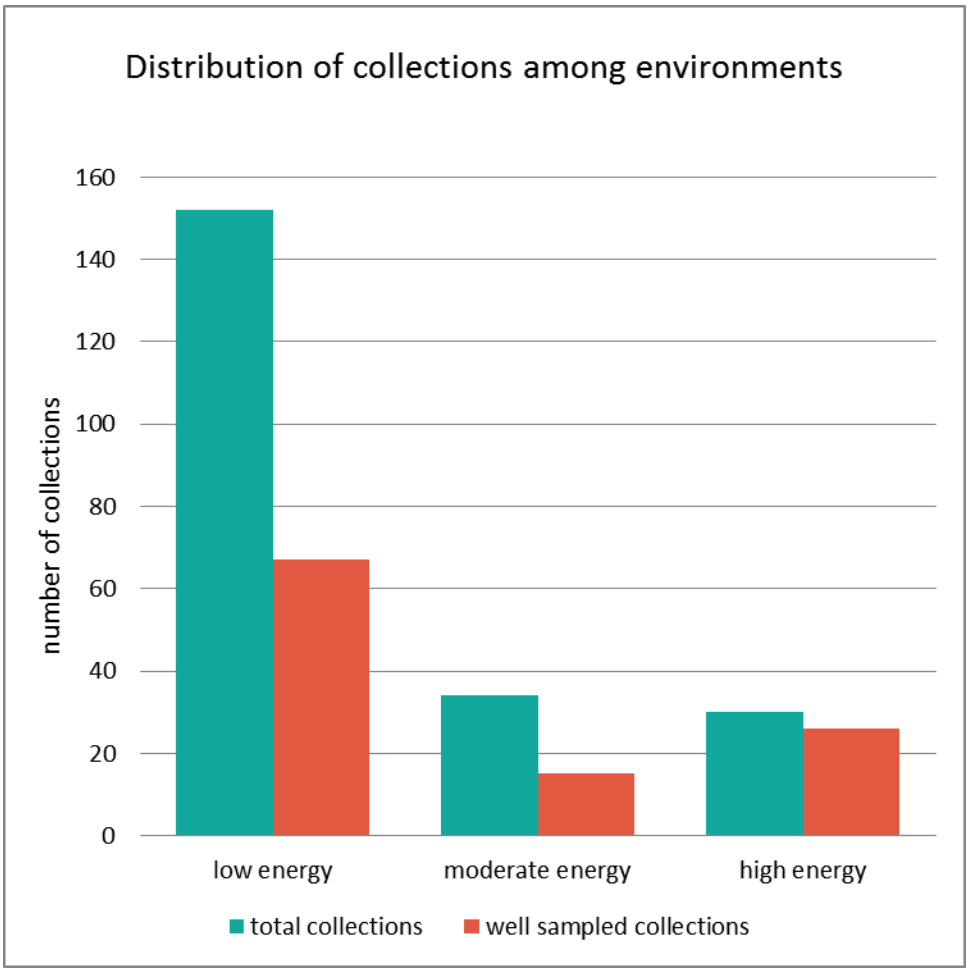


Figure 4. Relationship between number of specimens encountered in the field and collection richness. The relationship between field collection size and collection richness is triangular. Only large field collections have very high richness, low richness is encountered in small field collections and in some large field collections.

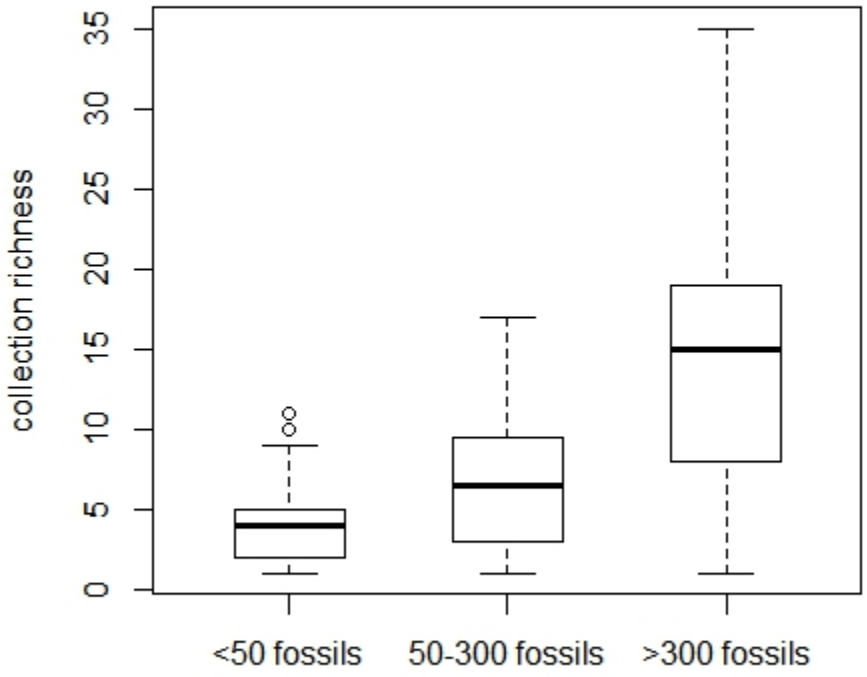


Figure 5 Fossils of early Albian angiosperm leaves from the western United States. Left: lobed leaflet of an angiosperm herb from a brown siltstone in the Kootenai Formation (MT) Right: lobed leaf of an angiosperm herb from a gray mudstone in the Cloverly Formation (MT).

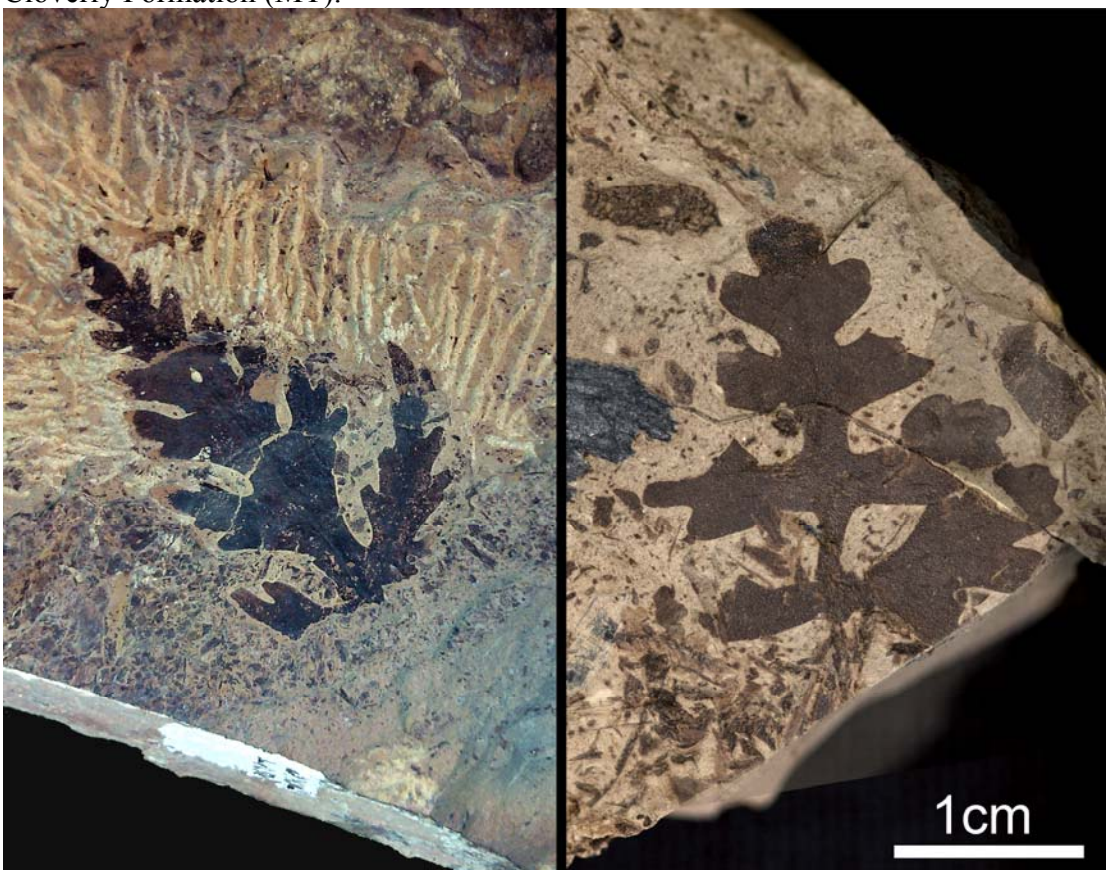


Figure 6. Proportion of Lower Cretaceous plant megafossil collections (n=259) that include angiosperms through time.

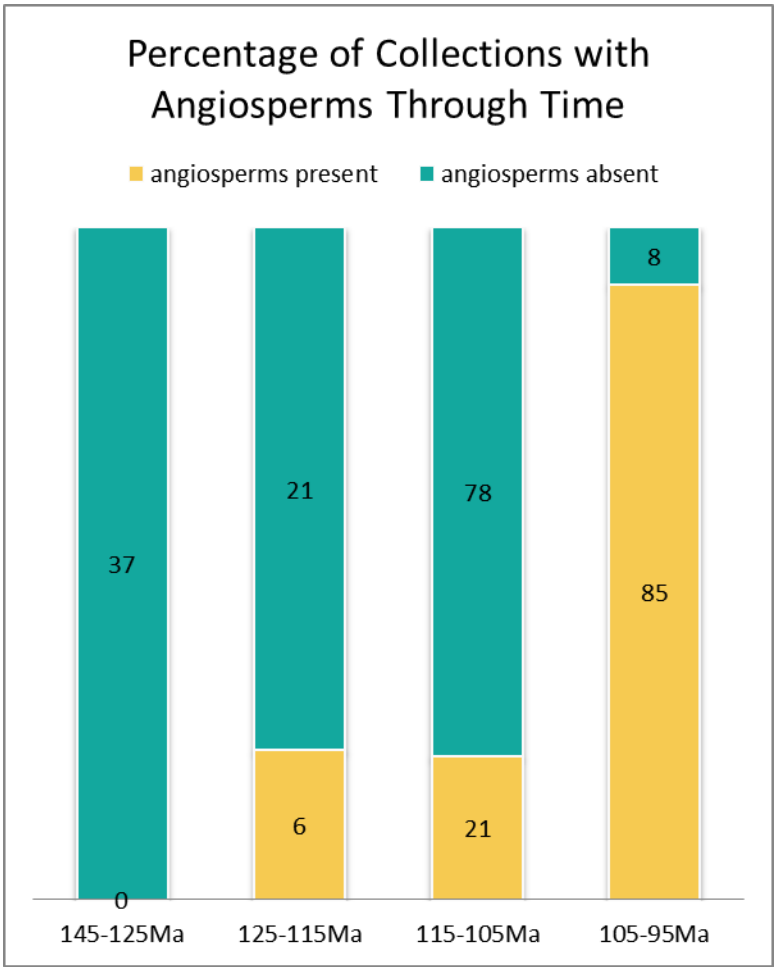


Figure 7. Proportion of collections dominated by major taxonomic groups. Lower Cretaceous plant megafossil collections are often dominated by conifer foliage, but angiosperms dominate many of youngest collections as well. The "Unknown/Other" category includes collections dominated by cycadophytes, ginkgophytes, and *Sageonopteris*, but also includes collections that are dominated by a fern or conifer. The the angiosperm-dominated collections in the 115-105Ma time bin are estimated as middle Albian, but these estimates are poorly constrained and may be too old.

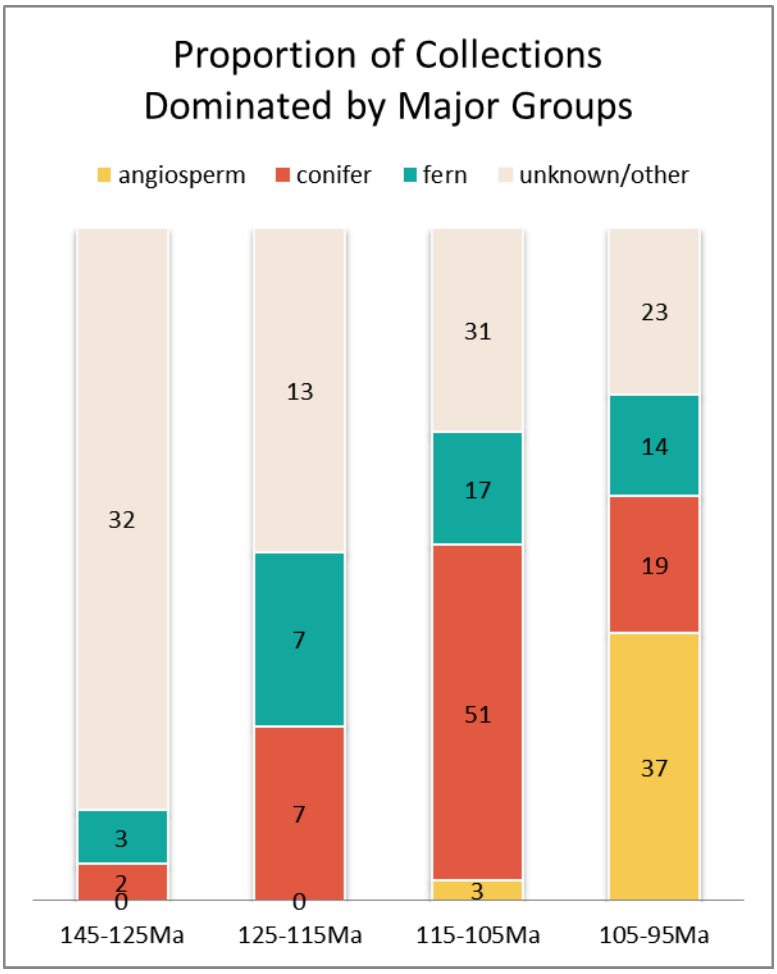
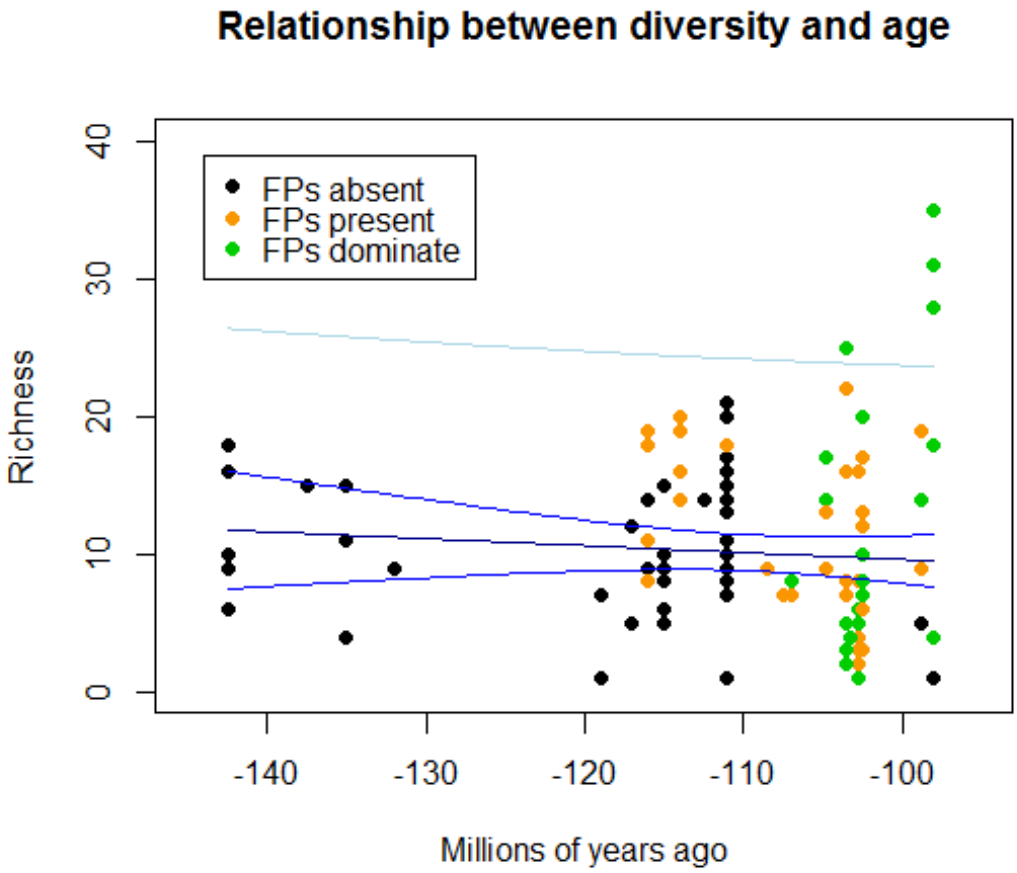


Figure 8. Morphotype richness of large collections from Lower Cretaceous deposits and the pattern of angiosperm abundance through time. A one-tailed permutation test for a increasing richness with decreasing age shows that that data are consistent with the null hypothesis that collection richness is not related to age (p=0.8). Angiosperms first occur in Aptian deposits (125-113Ma), but local angiosperm dominance becomes common much later. The age of the oldest angiosperm-dominated collection in this dataset is poorly constrained and may be too old.



Chapter 5: Plant megafossils from the Lower Cretaceous Cloverly and Sykes Mountain Formations (Wyoming, USA) and their bearing on early angiosperm evolution

Abstract

During the Early to mid-Cretaceous flowering plants (angiosperms) began a striking diversification. Studies of fossils from the Lower Cretaceous Potomac Group of the Mid-Atlantic coastal plain led to the hypothesis that both angiosperm diversity and environmental range increased from the Aptian to the Cenomanian, but rigorous tests of the hypotheses about early angiosperm ecology developed based on those studies have just begun. Here I use new plant fossil collections from the Lower Cretaceous Cloverly and Sykes Mountain formations of Wyoming to investigate changes in the diversity and environmental range of angiosperms during Neocomian to Late Albian time. Angiosperm fossils are not present in collections from the lower part of the Cloverly Formation (Fm.). One rare herbaceous angiosperm morphotype occurs in a gymnosperm and fern-dominated flora preserved in the upper part of the Cloverly Formation. Angiosperms are widespread, but generally rare in the Sykes Mountain Formation. Thus, floras from the Cloverly and Sykes Mountain formations document the arrival and spread of angiosperms in western North America during the Neocomian-late Albian.

Richness and evenness of collections from local sites are highly variable, with no clear trend of increasing richness from older, pre-angiosperm to younger, angiosperm-bearing floras. A comparison of sample-based collecting curves from sites in the lower and upper parts of the sequence shows that new species accumulate slightly faster in the angiosperm-bearing part of the sequence. At the current sampling level, neither curve approaches an asymptote. Multivariate dispersion of fossil sites in Jaccard distance-space shows no significant difference in beta diversity among sites in the lower as opposed to the upper part of the sequence. This suggests that beta diversity was also unchanged through the arrival of angiosperms. Data from the Cloverly and Sykes Mtn. Formations do not demonstrate major changes in plant diversity patterns during the Neocomian-Late Albian; however, the broad distribution of angiosperm species suggests that by the Albian angiosperms diversified into a wide range of habitats.

Introduction

Flowering plants (angiosperms) comprise over three quarters of land plant diversity, but they diversified relatively recently in geologic time. Whereas the four living groups of gymnosperms are represented by fossils that date back to the Paleozoic (Taylor et al., 2008), over 250 Million years ago (Ma), the oldest fossils of crown-group angiosperms date to the Early Cretaceous, some 130-134Ma (Hughes et al., 1991; Brenner, 1996; Segev, 2009). This difference implies an ancient origin of the angiosperm stem-lineage (Hochuli and Feist-Burkhardt, 2013), but the appearance of fossils attributable to crown groups and the sequential appearance of fossils with successively more derived character states in Cretaceous deposits provides strong

evidence that the rapid diversification of angiosperms began during the Early Cretaceous (Friis et al., 2010; Doyle, 2012; Zhang et al., 2014).

Despite the ecological importance of modern angiosperms, there have been relatively few studies that take a quantitative approach to understanding how Early Cretaceous plant communities changed with the diversification of angiosperms during that time. Here, I show that quantitative data on angiosperm abundance from the Lower Cretaceous of Wyoming can be used to test long-standing hypotheses regarding early angiosperm ecology.

The Cloverly Formation (Fm.) and the Sykes Mountain Fm. comprise the Lower Cretaceous non-marine sequence in the Bighorn Basin, Wyoming. Plant megafossils can be found throughout the two formations, but the floras have received little attention. Knowlton (1916) published a brief account of plant macrofossils from lower part of the Cloverly Fm. (then considered Morrison Fm.), and more recently others reported plant fossils from the upper Cloverly and Sykes Mountain Fms. (Wilborn, 2006; Walton, 2007).

Here I test the hypothesis that angiosperms were restricted to a subset of available habitats during the Albian, and that angiosperm abundance was greater in disturbed than stable environments. Next I evaluate the hypothesis that angiosperms displaced non-angiosperms by comparing the species richness of collections with and without angiosperms. Finally, I compare the variation in sample composition (beta diversity) before and after the appearance of angiosperms in order to evaluate the effect of the angiosperm diversification on plant communities at broader spatial scales.

Methods

Geologic Setting

The Lower Cretaceous Cloverly and Sykes Mountain Fms. comprise 20-80 m of sandstone, siltstone, mudstone, and claystone deposited in fluvial and lacustrine settings. This sequence overlies the upper Jurassic Morrison Fm. and underlies the late Albian Thermopolis Shale Fm. The Cloverly and Sykes Mountain formations have been subdivided into members or informal units by several authors with slight differences (Moberly, 1960; Ostrom, 1970; Meyers, 1992). Here, I follow the system depicted in Figure 1, based on the work of Moberly (1960). The plant fossils in this study came from the lower part of the Little Sheep Mudstone Member (hereafter lower Cloverly), the upper part of the Little Sheep Mudstone Member (hereafter upper Cloverly), and the "Greybull interval" of the Sykes Mountain Fm. (equivalent to Ostrom's unit VII of the Cloverly Fm.), following the recommendation of Kvale (1986; Kvale and Vondra, 1993). Exposures of the Cloverly and Sykes Mountain Formations used in this study are in the Bighorn Basin of northern Wyoming and southern Montana (Figure 2).

The Cloverly Formation is comprised of continental fluvial, lacustrine, and playa deposits laid down in an overfilled foreland basin setting by northeast trending anastomosing and meandering channels that brought in sediment from the Sevier mountains to the west and southwest (Winslow and Heller, 1987; DeCelles and Burden, 1992; Meyers et al., 1992; Elliott Jr. et al., 2007; Leier and Gehrels, 2011). pedogenic features in the Cloverly Formation including carbonate nodules and pseudo-slickensides, indicate seasonal to semi-arid conditions (Elliot et al. 2007) that

may be explained at least in part by a rain shadow from the Sevier mountains to the west (Elliot et al. 2007), particularly considering that a continental-scale estimation of Albian precipitation and evaporation based on sphaerosiderite d18O values from paleosols suggests that precipitation exceeded evaporation north of about 30° paleolatitude (Ufnar et al., 2004). The Sykes Mountain Formation is composed of comprised of continental fluvial to marginal marine deposits laid down as the western interior seaway transgressed from the north (Vuke, 1984; Winslow and Heller, 1987; Kvale and Vondra, 1993). Large meandering channel systems supplied sediment from the east onto the coastal plain (Kvale and Vondra, 1993), and this may have compensated for low precipitation values by supplying water for the low-lying habitats where plant fossils are preserved.

The age of the Cloverly and Sykes Mountain Formations is poorly constrained because of lateral facies changes and numerous unconformities. Pollen samples from a bed in the lower part of the Cloverly Fm. near Ten Sleep, WY, include *Trilobosporites* and *Concavissimisporites*, and lack angiosperm pollen (Nolan, 2000; Hu, personal communication, 2012; personal observation). A similar palynoflora was reported from the lower part of the Cloverly in the Wind River Basin (DeCelles and Burden, 1992). This indicates that the lower Cloverly dates to the pre-Aptian Early Cretaceous (Thusu and Van Der Eem, 1985; Fensome, 1987). A recent ash sample from the upper Cloverly Formation yielded a date of 111Ma (Carrano, pers com 2014). Detrital zircons from the Greybull interval of the overlying Sykes Mtn. Formation in Northern Wyoming provide a maximum age for the unit of 104.0+/-0.2Ma (D'emic and Britt, 2008). These data indicate that the Cloverly-Sykes

Mountain series spans more than 20Ma and captures the appearance of angiosperms in the fossil record of North America and the radiation of eudicot angiosperms (Jud and Hickey, 2013).

Data Collection and Analysis

I collected fossil leaves and shoots, as well as lithological and sedimentological data, from sites throughout the Cloverly and Sykes Mountain formations in the Bighorn Basin, WY, USA over the course of four field trips during 2010-2013 with the help of several field assistants (Appendix IV). At each site we made a small quarry using hand tools, and I recorded geographic coordinates and assigned a unique number to the site. I also assigned a collection number to every fossiliferous block collected from each site during a single visit. All of the blocks also received unique USNM numbers in the laboratory; blocks that were broken or split along bedding planes to reveal parts and counterparts of plant megafossils were grouped together and received the same USNM number. All of the plant fossil collections included in this study are curated in the Department of Paleobiology at the National Museum of Natural History, Smithsonian Institution, Washington DC, USA.

At each site I observed the geometry of the fossiliferous deposit, and then categorized fossiliferous rock by grain size, primary bedding, organic content, and color (Table 1). I used the sedimentary information to infer the environment of deposition for each site. In general, the preservation of the plant fossils suggests minimal transport from the site of growth to the site of burial and preservation, and therefore the features of the depositional environments can be assumed to reflect local and regional environmental conditions that are relevant to understanding the

environment of growth for the original plant community (Spicer and Wolfe 1987; Greenwood 1991; Davies-Vollum and Wing, 1998).

First, I sorted each identifiable plant fossil into one of seven broad taxonomic categories: horsetail, fern, conifer, cycadophyte, ginkgophyte, angiosperm, and incertae sedis. Then, I segregated the fossils into operational taxonomic units (morphotypes) using leaf architectural features such as the shape of the leaves, leaflets, or pinnae, features of the leaf margin, and the primary and secondary vein framework (Ellis et al., 2009). I assigned an informal alphanumeric code to each morphotype for paleoecological analysis (Appendix I). The first two letters of each morphotype code (CV) stand for Cloverly, the second letter or letters refers to the broad taxonomic category of the morphotype (A=angiosperm, F=fern, Co=conifer, Cy=cycadophyte, G=ginkgophyte, and E=horsetail), and the number identifies a distinct morphotype in the same broad taxonomic category.

I created a presence-only matrix of sites and species using the data in Appendix II and conducted an NMDS analysis of the matrix to determine if there are compositionally distinct groups of collections that correlate with geological age or inferred depositional environment. I also conducted an NMDS analysis of sites from the Sykes Mountain Fm. alone to determine if floristic composition within the younger unit varied with depositional environment.

I conducted a census and collected abundance data from 6 sites in the Sykes Mountain Fm. 1 site in the upper part of the Cloverly Fm., and 4 sites from the lower part of the Cloverly Fm. I quantified abundance using three different methods and I evaluated the relative performance of each approach. The first method, known as the

quadrat method (Pfefferkorn et al., 1975), involves counting the proportion of blocks or hand specimens from a site that bear a particular morphotype. The second method is to count the total number of plant fragments assigned to each morphotype at a site. The third method is to estimate the relative cover of the fragments belonging to each morphotype on each block. For the third method, I used a semi-quantitative scale to estimate relative cover following a modification of the Braun-Blanquet method (Braun-Blanquet, 1932). I treated each block from a site as a quadrat and estimated the contribution of each morphotype to the total observed photosynthetic area on each block. A score of "1" means <10%, "2" means 10-25%, "3" means 25-50%, "4" means 50-75%, and "5" means 75-100%. Separately for each method I summed the scores for each morphotype across all blocks at a site to obtain an abundance distribution for the site. I evaluated the relative performance of the different abundance metrics by comparing the three rank order abundance distributions obtained for each site.

To test the hypothesis that the angiosperm diversification increased local community richness I compared diversity estimators obtained for each of the 11 censused collections. To account for the effects of sample size, I calculated rarified richness at 100 specimens (S_{100}) (Hurlbert, 1971) for each of the 11 sites with abundance data. I also calculated two abundance-based diversity metrics: Hulbert's PIE (Olszewski, 2004) and Fisher's alpha (Fisher et al., 1943).

Finally, I tested for a change in beta richness associated with the appearance of flowering plants using two approaches. First I created sample-based collection curves for the lower Cloverly and the Sykes Mountain Formation using the R package

vegan (Oksanen et al., 2013). Second, I conducted a test for homogeneity of multivariate dispersion (Anderson et al. 2011) implemented using the function permDisp in the R package vegan (Oksanen et al., 2013). This involves calculating Jaccard's dissimilarity, a presence-absence metric, between all pairs of sites in the lower Cloverly and the Sykes Mountain Formation separately, and then calculating the average distance between sites and their group centroid. A P-value is then obtained by permuting the least-squared residuals (Anderson et al., 2006). I used 22 collections from the Sykes Mountain Fm. and 5 collections from the lower part of the Cloverly Fm. after combining all occurrences from the lake deposit into a single site, thereby treating the lake as a single depositional event.

Results

I collected ~4700 identifiable fossils on 1037 hand specimens from 28 sites and segregated the fossils into 96 morphotypes using leaf architectural characters (Appendix I). The fossils include leaves of 37 non-monocot angiosperms, 45 ferns, 7 conifers, 2 ginkgophytes, 7 cycadophytes, and 1 horsetail of undetermined affinity to higher taxonomic level. With the exception of one morphotype that occurs in a collection from the upper part of the Cloverly Fm., all of the angiosperm morphotypes are restricted to the Sykes Mountain Fm. I estimate that at least 20 of the angiosperm morphotypes are eudicot angiosperms. Although the angiosperms are species-rich in the Sykes Mountain Formation, they are generally rare. Most angiosperm morphotypes occur at only one site (Figure 3) and many are represented by very few specimens. On average, angiosperm morphotypes occur at 1.6 sites

whereas ferns occur at 2.1 sites and the one conifer morphotype occurs at 18 out of 21 sites.

I recognize three categories of depositional environment based on the geologic data that I collected. Fine-grained channel fills are lenticular, flat laminated, brown or gray siltstone units up to ~10 meters across and ~1-8 meters thick. Collections from these units may include fossils of freshwater snails and clams, as well as relatively complete herbaceous angiosperms. These are low-energy deposits and most of the plant fossils preserved at these sites were not transported far prior to preservation. I interpret these sites as low-lying wetland and pond habitats in which sediment accumulated following channel abandonment. The high energy deposits are ripple-laminated or massive sandy beds that preserve small, fragmentary fossils or folded and torn leaves. Plant remains preserved in these deposits were probably transported from the original site of growth into topographical lows on the floodplains. Some of these deposits appear to be part of small-scale channel-fill complexes, whereas others are thin (less than 1m), laterally extensive (tens of meters), and bounded by fine-grained floodplain paleosols. In interpret these high energy deposits as crevasse-splay deposits (Slingerland and Smith, 2004). The third depositional setting, a shallow lake, was found only in a single bed in the lower Cloverly Fm. near Ten Sleep, Wyoming. This bed is a laterally extensive (>2 km), gray mudstone with flat lamination. It also contains barite nodules, and I saw abundant algal debris in palynological preparations. Table 1 shows the sedimentological features associated with each depositional environment category, and Table 2 shows the distribution of sites among depositional categories in each stratigraphic interval.

The lacustrine facies in the lower part of the Cloverly Fm. provides a unique opportunity to test the hypothesis that angiosperms increased alpha diversity using plant megafossil collections. With plant fragments coming in from around the shores of the lake, the cumulative richness of collections from the lake deposits should reflect a large area of original vegetation, and therefore should record high local diversity, if present, By contrast, collections from fine-grained channel-fill deposits in the Sykes Mountain Fm. are local (parautochthonous) samples of wetland or pond-margin vegetation. Taphonomic effects thus bias against finding an increase in richness between the lake assemblage and any given channel-fill assemblage. Based on 10 different collections and over 1000 identifiable plant fossils, the pooled morphotype richness of the lacustrine deposit is 15 morphotypes. This pooled richness is less than that from individual highly localized fine grained channel fill assemblages in the later time interval, which ranges up to 22 morphotypes determined from over 1000 identifiable fossils. This result is consistent with the hypothesis that the diversification of flowering plants increased local species richness in at least some communities.

In the Sykes Mountain Fm. angiosperm abundance does show an association with local depositional environment. Collections from the laterally extensive, thin sandy, splay deposits are overwhelmingly dominated by a single angiosperm morphotype. By contrast, the wetland and pond deposits are dominated by conifer or fern foliage with the exception of one site that is angiosperm dominated (NAJ 1102). Based on the cordate base, perpendicular petiole insertion, and inflated petioles, the

most abundant morphotype at the angiosperm-dominated site was probably a marginally aquatic herb of low-stature, rather than a large tree or shrub.

An NMDS analysis of all the presence-only data shows two distinct clusters of sites based on community composition; one for the lower Cloverly Fm. sites (pre- to early Aptian) and the other for the upper Cloverly Fm. and Sykes Mountain Fm. sites Albian) (Figure 4). An NMDS analysis of sites from the Sykes Mountain Fm. alone yields a single cloud of points based on composition of the collections (Figure 5). However, the sites in the laterally extensive splays that preserve folded and torn leaves are compositionally similar and plot together within the large cluster.

For the eleven sites censused sites rank order the three methods of quantification performed similarly, with minor switching in the rank order of adjacent pairs of morphotypes that had intermediate abundance. The quadrat method (Pfefferkorn et al., 1975) provided the least resolution, particularly for small collections and for sites with high density of fossils in the rock matrix. This was because morphotypes that occur on the same number of blocks received the same score even if one morphotype was much larger or represented by more fragments than another.

The sample standardized diversity estimates obtained from the 4 lower Cloverly Fm. collections fall within the range obtained for the 6 Sykes Mountain Fm. Thus, these data do not support the hypothesis that the diversification of flowering plants increased local species richness; however, given the small sample size, only a very strong signal of diversity increase was detectable.

I also compared the variation in site composition (beta diversity) between sites from the Sykes Mountain Fm. and sites from the lower part of the Cloverly Fm. using two approaches. First, I generated sample-based rarefaction curves for the two groups of sites (Figure 6). These curves show that the rate of species accumulation remains high for both groups, and that additional collections will continue to yield new morphotypes. The curve generated from the lower Cloverly collections is shallower than the curve generated from the Sykes Mountain collections, but the observed species richness of 28 morphotypes in all 11 lower Cloverly collections still falls within confidence interval around the curve generated from the Sykes Mountain Fm. collections. Second, the test for homogeneity of multivariate dispersion yielded similar dispersion estimates despite the difference in sample size between the two groups. The average dispersion for the Sykes Mountain Fm. collections was 5.841, and for the lower Cloverly Fm. collections it was 5.831 (Figure 7 & 8), the difference is not significant (P=0.973). Therefore, I fail to reject the null hypothesis of no difference in beta diversity between the pre-angiosperm and angiosperm-bearing collections.

Discussion

The collections from the Cloverly and Sykes Mountain Formation span at least 20Ma of plant evolution during the Early Cretaceous and there is nearly complete floral turnover from the lower part of the Cloverly Fm. to the Sykes Mountain Fm. Importantly, this time interval spans the appearance of crown-group angiosperms in North America and the diversification of eudicot angiosperms during the Early Cretaceous (Jud and Hickey, 2013), providing an opportunity to study plant

community change across a major evolutionary transition in deep time in one geographic area.

Angiosperm fossils are absent from the lower Cloverly collections, but nearly every collection from the Sykes Mountain Fm. includes at least some angiosperm fossils, regardless of lithology. This means that by Albian angiosperms were widespread among the available habitats in or near sites of deposition. The possibility that angiosperms were restricted to habitats with moderate to high frequency disturbance and high water availability cannot be ruled out because all of the habitats sampled were fluvial habitats on a coastal plain. This pattern is qualitatively similar to that reported by Doyle and Hickey (1976; Hickey and Doyle, 1977) for the Potomac Group and by Coiffard et al. (Coiffard et al., 2006, 2007, 2008; Coiffard and Gomez, 2009) for Western Europe. Both teams found that by the Albian angiosperms had spread to nearly all habitats except fine-grained, carbonaceous backswamp deposits, which do not occur in the Sykes Mountain Fm.

The diversification of angiosperms probably increased local species richness in some habitats by augmenting the diversity of small, herbaceous plants that could colonize and quickly reproduce in small patches of available substrate made available by disturbance events, thus avoiding direct competitive interaction. However, I did not detect an increase in species richness associated with the appearance of angiosperms using leaf megafossil collections after sample standardization. This could be because fossil leaf assemblages from parautochthonous fluvial depositional environments like those described in this study are dominated by local plants (Davies-Vollum and Wing, 1998), and that the number of species in a collection is primarily

influenced by the number of individual plants growing in the small area of vegetation represented in the sample (Burnham, 1993). However, if most angiosperms were small herbaceous plants this may not be a problem because their small size would permit the coexistence of many individuals, and thus more species. Alternatively, it could be that collections consisting of several hundred leaves do not provide sufficient coverage to detect species that are represented by few individuals that shed few leaves. This could lead to significant bias because rare species can contribute strongly to species richness estimates (Magurran, 2004; Jost, 2006). In another study, Coiffard et al. (Coiffard et al., 2006, 2007, 2008; Coiffard and Gomez, 2009) found that on average angiosperm bearing collections from floodplain habitats were more species-rich than older collections without angiosperms or other coeval collections from different habitats; however, local species richness is strongly associated with number of specimens encountered, which the authors did not control. Despite these problems, the comparison between the collections from the lacustrine facies in the lower Cloverly Fm. and the pond and wetland collections of the Sykes Mountain Fm. provide some support for increased alpha diversity during the Early Cretaceous.

The appearance of angiosperm-dominated local assemblages in the mid-late Albian appears to reflect a real ecological change in vegetation structure, which lagged millions of years behind the initial diversification of crown-group angiosperms and the appearance of eudicot angiosperms. Whereas species richness estimates are strongly influenced by sample size if there are many rare species, Patterns of ecosystem dominance are more robust to sample size. Collections from the laterally extensive crevasse-splay deposits in the Sykes Mountain Fm. are consistently

dominated by angiosperm foliage from one or two morphotypes, whereas only one site from a fine-grained pond or wetland deposit was angiosperm-dominated (NAJ 1102), and the most common plant at that site is a low-stature marginally aquatic herbaceous angiosperm. These results are similar to the findings of Doyle and Hickey (1977), who reported collections from some mid-late Albian sites in or closely associated with high energy deposits are dominated by angiosperm foliage. One early Albian site from the Potomac Group was also probably dominated by fossils of *Vitiphyllum*, but *Vitiphyllum* was a low-stature herbaceous plant (Fontaine, 1889).

It is likely that the diversification of angiosperms increased beta diversity across edaphic, physiographic, and disturbance gradients. Although I did not find a significant difference in cumulative species richness between the lower Cloverly Fm. and the Sykes Mountain Fm. using site-based rarefaction analysis, the difference in slope of the two curves suggests that the diversity of the lower Cloverly Fm. will plateau earlier than the diversity of the Sykes Mountain Fm. The inclusion of additional sites from the lower Cloverly Fm. in another test for homogeneity of multivariate dispersion would provide a strong test for increased beta diversity in the Albian compared to the Neocomian.

Tables and Figures

Figure 1. Map of the Cloverly Formation and Sykes Mountain Formation outcrop in northern Wyoming. Collection sites are marked with circles.

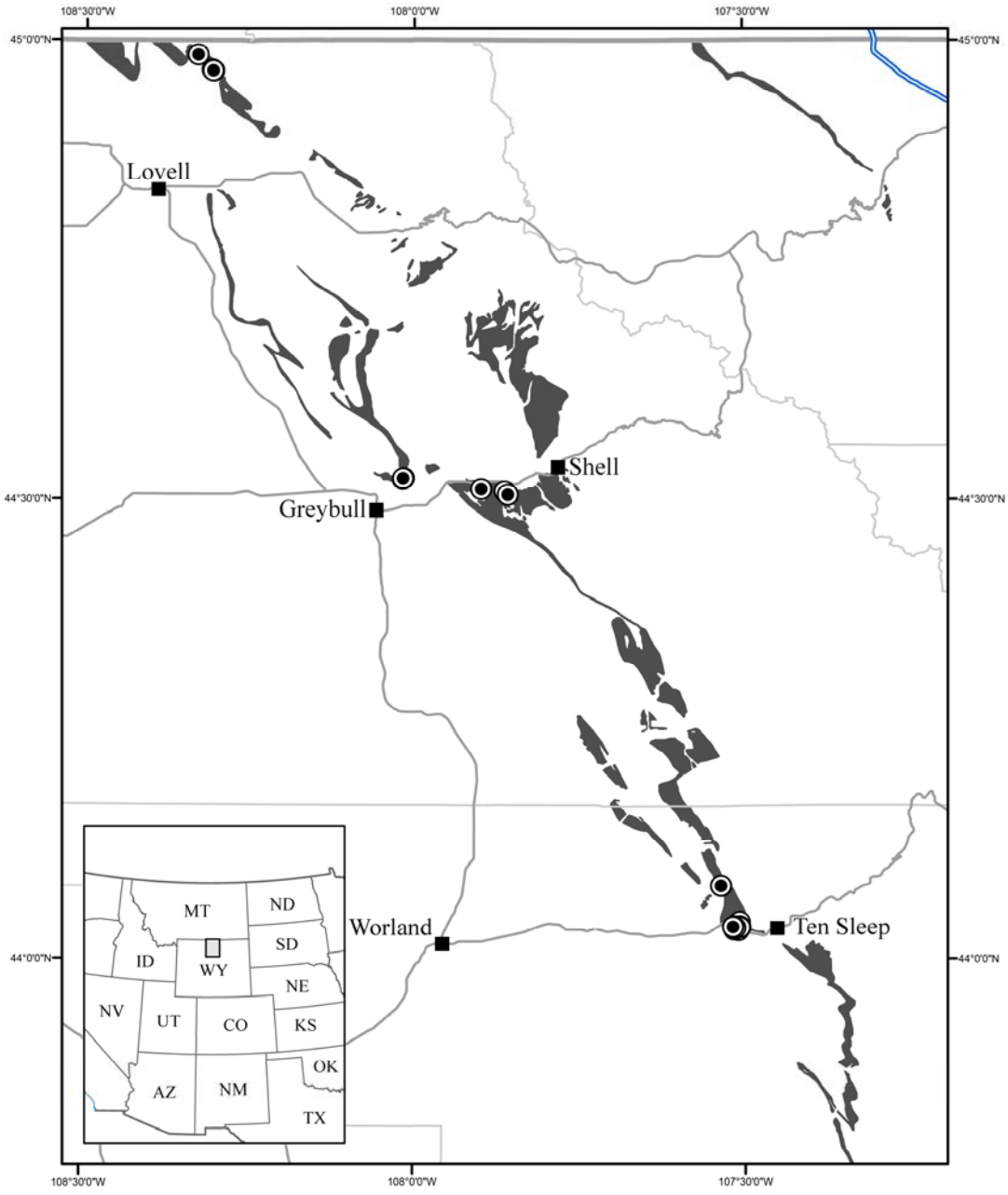


Figure 2. Generalized stratigraphic section of the Cloverly and Sykes Mountain formations in the Bighorn Basin comparing the stratigraphic systems of Moberly (1960) and Ostrom (1970). Note that fossil sites are found at roughly three different stratigraphic levels. In the northern part of the basin, Ostrom's unit IV is equivalent to the Pryor Conglomerate and is the lowest unit in the Cloverly Fm. In the southern part of the basin near Ten Sleep, the Pryor is absent and the lower part of the Little Sheep Mudstone .Member overlies the Morrison Fm.

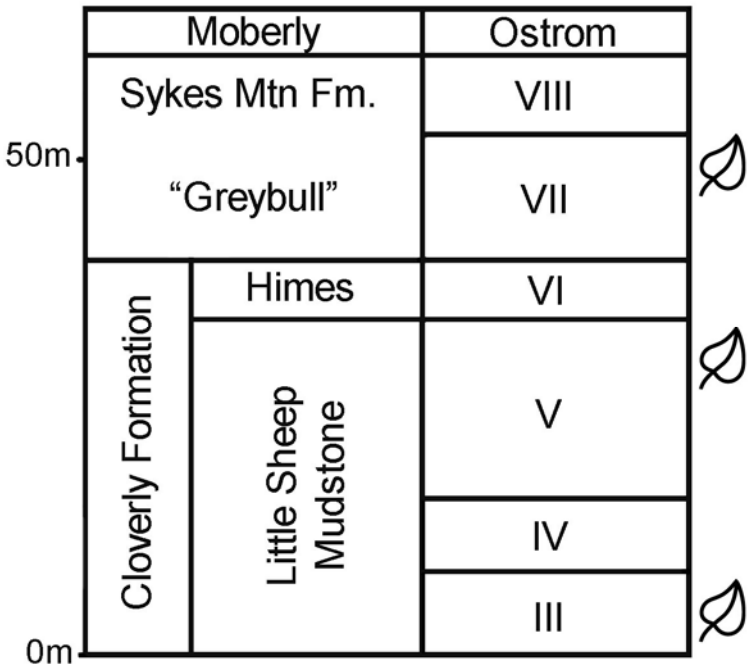


Figure 3. Occupancy distribution showing the distribution of morphotype occurrences by site for the Greybull interval of the Sykes Mountain Formation. Note that most morphotypes, and in particular most angiosperm morphotypes, occur at only one site.

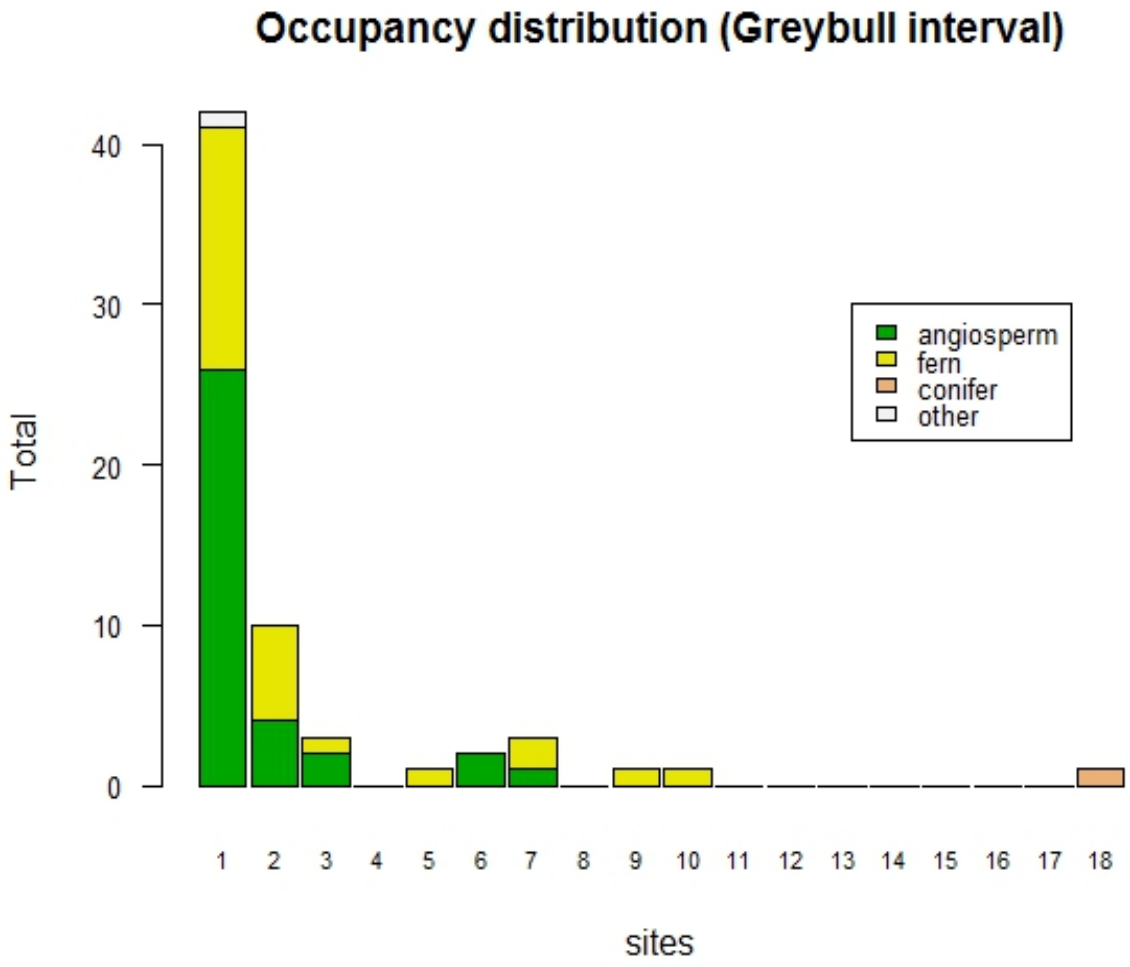


Figure 4. NMDS ordination of sites in morphotype-space. Note the clear separation between collections from the lower part of the Little Sheep Mudstone member (Unit III) and the collections from the upper Little Sheep Mudstone member and the Greybull interval (Units V and VII).

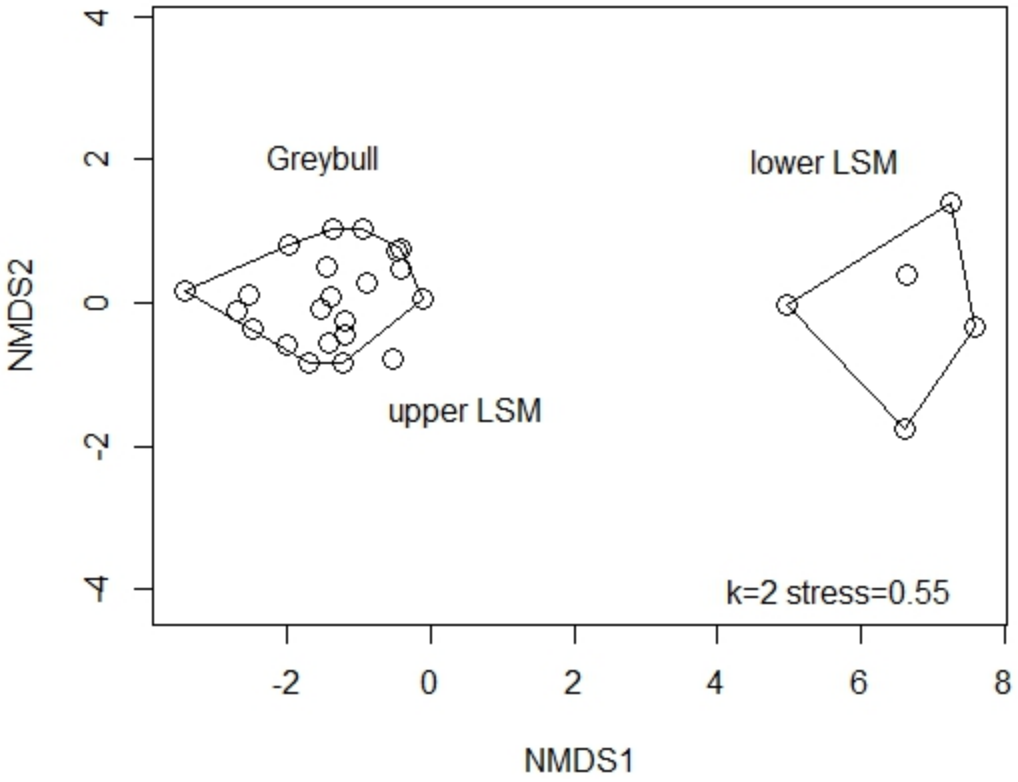


Figure 5. NMDS ordination of sites from the Sykes Mountain Formation. Proximity of sites in multivariate space reflects similarity of morphotype composition. The four sites in blue on the right side of the plot have similar composition. They also are dominated by the same angiosperm morphotype and they all come from thin sandy beds.

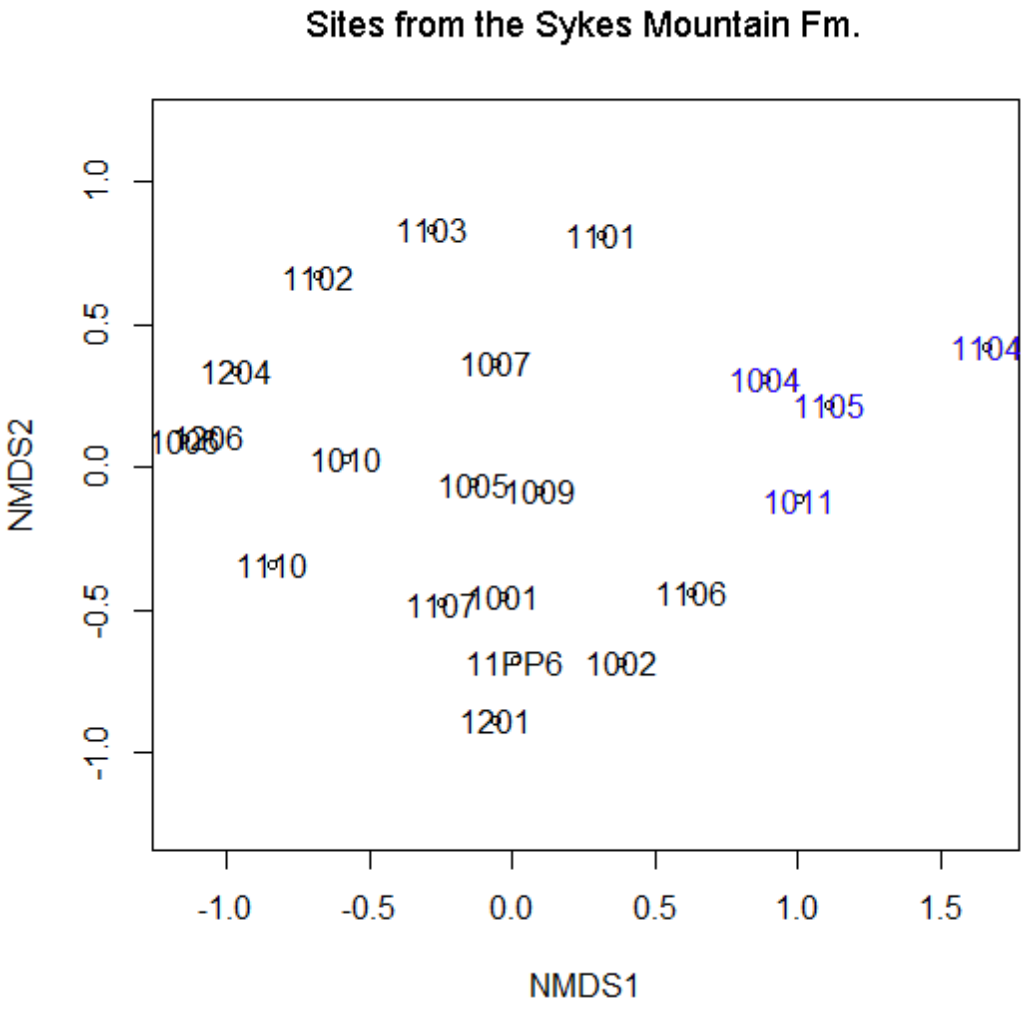


Figure 6. Site-based species accumulation curves for the pre-angiosperm collections from sites in the lower part of the Cloverly Formation (orange and green) and the angiosperm-bearing sites in the Sykes Mountain Formation (yellow and blue). Note that the slope of the pre-angiosperm curve is shallower, but also that it falls within the confidence interval around the angiosperm curve.

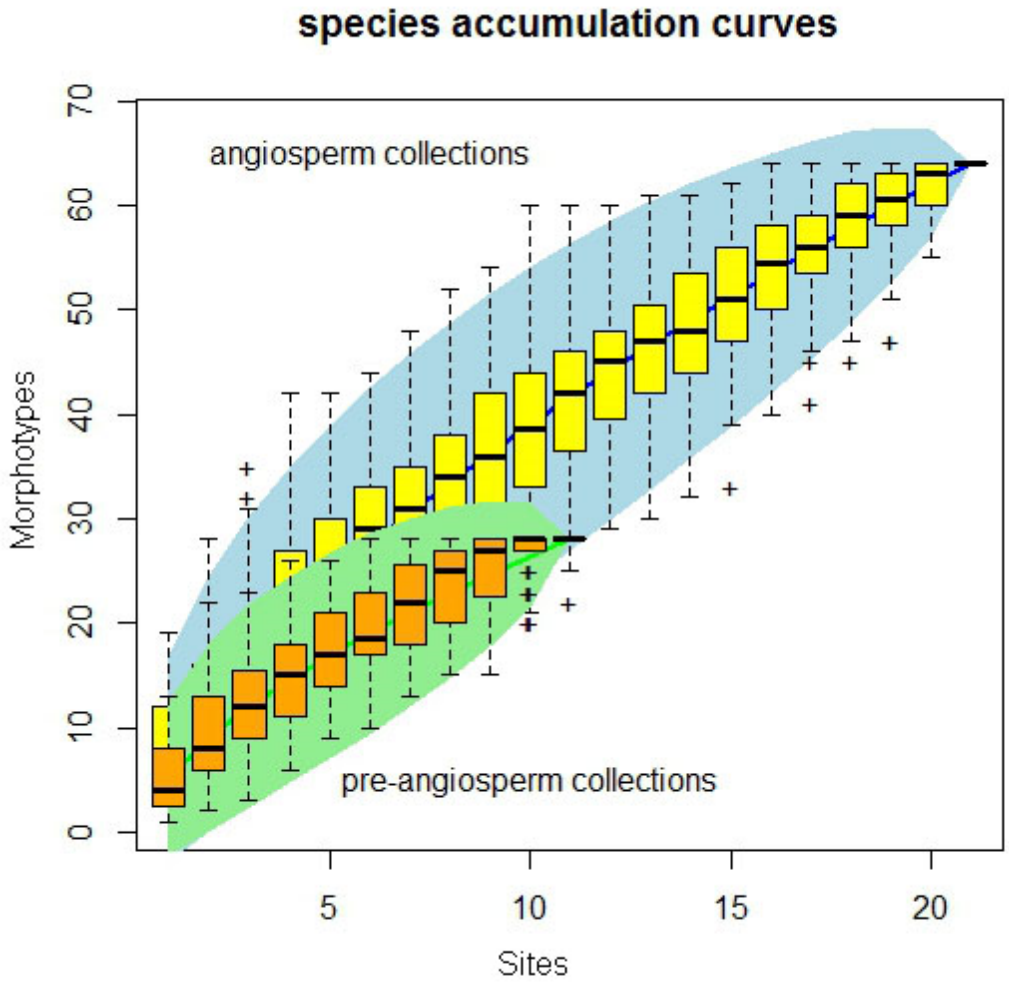


Figure 7. Multivariate dispersion of sites from the Cloverly Formation based on the Jaccard dissimilarity metric. The sites in the upper group are in the Greybull interval and include angiosperms, whereas the sites in the lower group are in the lower Little Sheep Mudstone member of the Cloverly Fm. and lack angiosperms. The difference in dispersion between the two groups is not statistically significant.

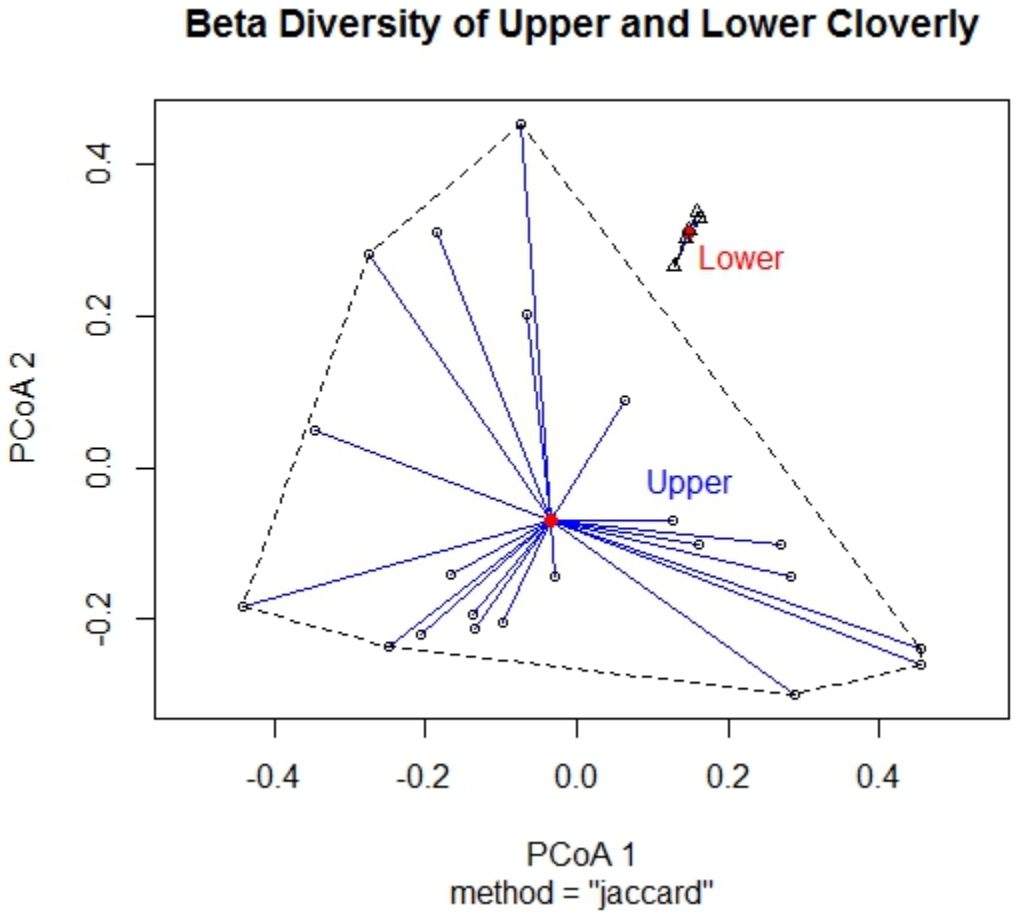
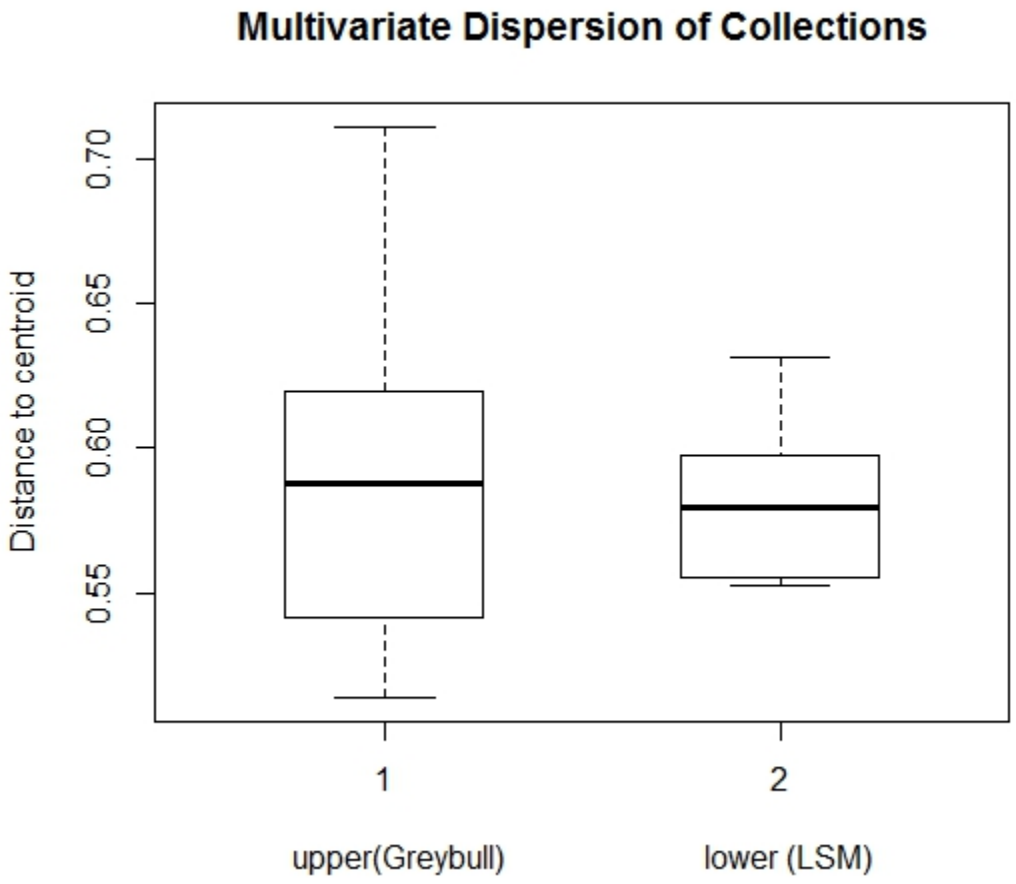


Figure 8. Boxplot of the distances to centroid in for each group of sites



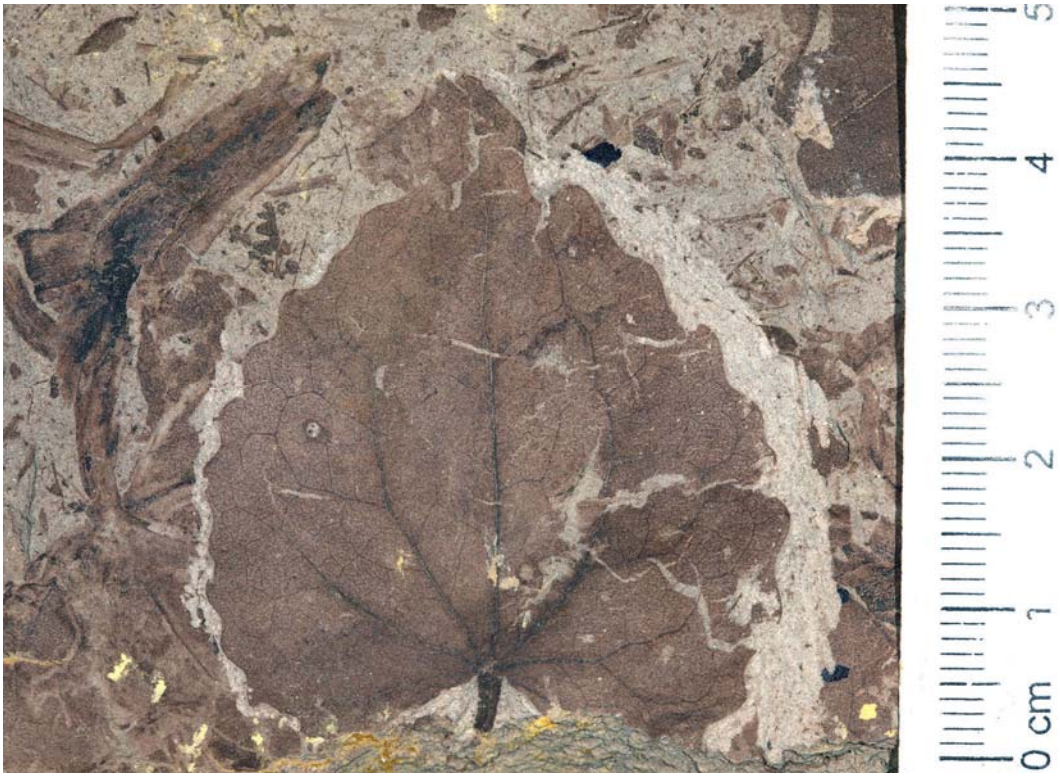
Appendix I

Descriptions of morphotypes used in Chapter 5

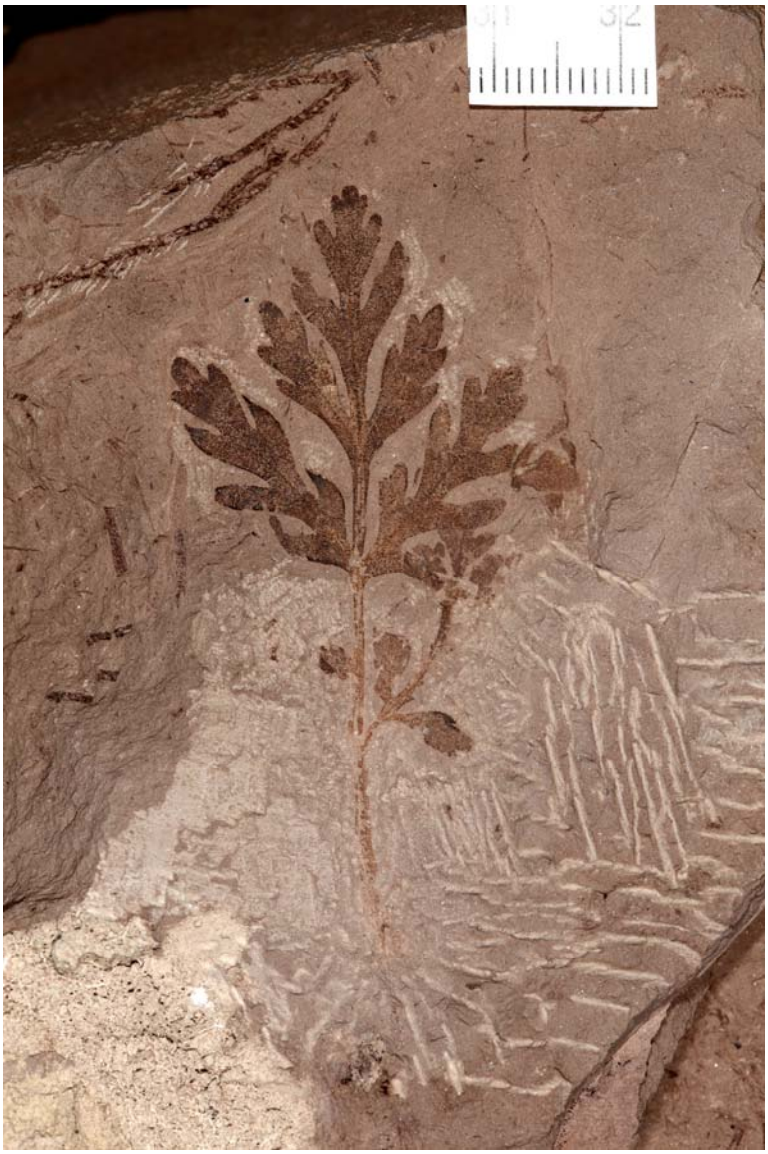
Angiosperms

Format of angiosperm descriptions:
Morphotype ID, USNM Exemplar
Description: Leaf organization, petiole features. Laminar size, L:W ratio, shape. Margin entire, lobed or serrate. Apex angle, shape, symmetry, base angle, shape, symmetry.
Primary venation, basal veins. Secondary vein framework, minor secondary veins, secondary vein angle, spacing; interior secondary veins, minor secondary veins, marginal secondary vein. Intercostal tertiary vein fabric, epimedial tertiarties, exterior tertiary course. Quaternary vein fabric, FEVs.
Tooth spacing, orders of teeth, teeth per centimeter. Sinus shape, tooth shape. Principle vein termination, accessory veins, tooth apex.
Interpretation: habit, clade

Morphotype CVA1, USNM 554064
Description: Leaf simple, marginal petiolate, petiole perpendicular to the blade, inflated. Laminar size notophyll. L:W ratio 1:1, shape ovate. Margin unlobed, serrate, apex acute, straight, symmetrical, base reflex, cordate, symmetrical.
Primary venation basal actinodromous, (3)5-7 basal veins. Secondary vein framework festooned semicraspedodromous, secondary vein angle acute, secondary vein spacing decreases distally. Intercostal tertiary vein fabric irregular reticulate, epimedial tertiaries reticulate, exterior tertiary course looped. Quaternary vein fabric irregular reticulate, FEVs not visible.
Tooth spacing regular, one order of teeth, at 3 teeth per centimeter. Sinus shape rounded, tooth shape convex/convex. Principle vein termination at apex of tooth, accessory veins running from sinus, tooth apex cassidate.
Interpretation: herbaceous, eudicot (cf. *Eomecon*, *Cercidiphyllum*, *Tetracentron*)

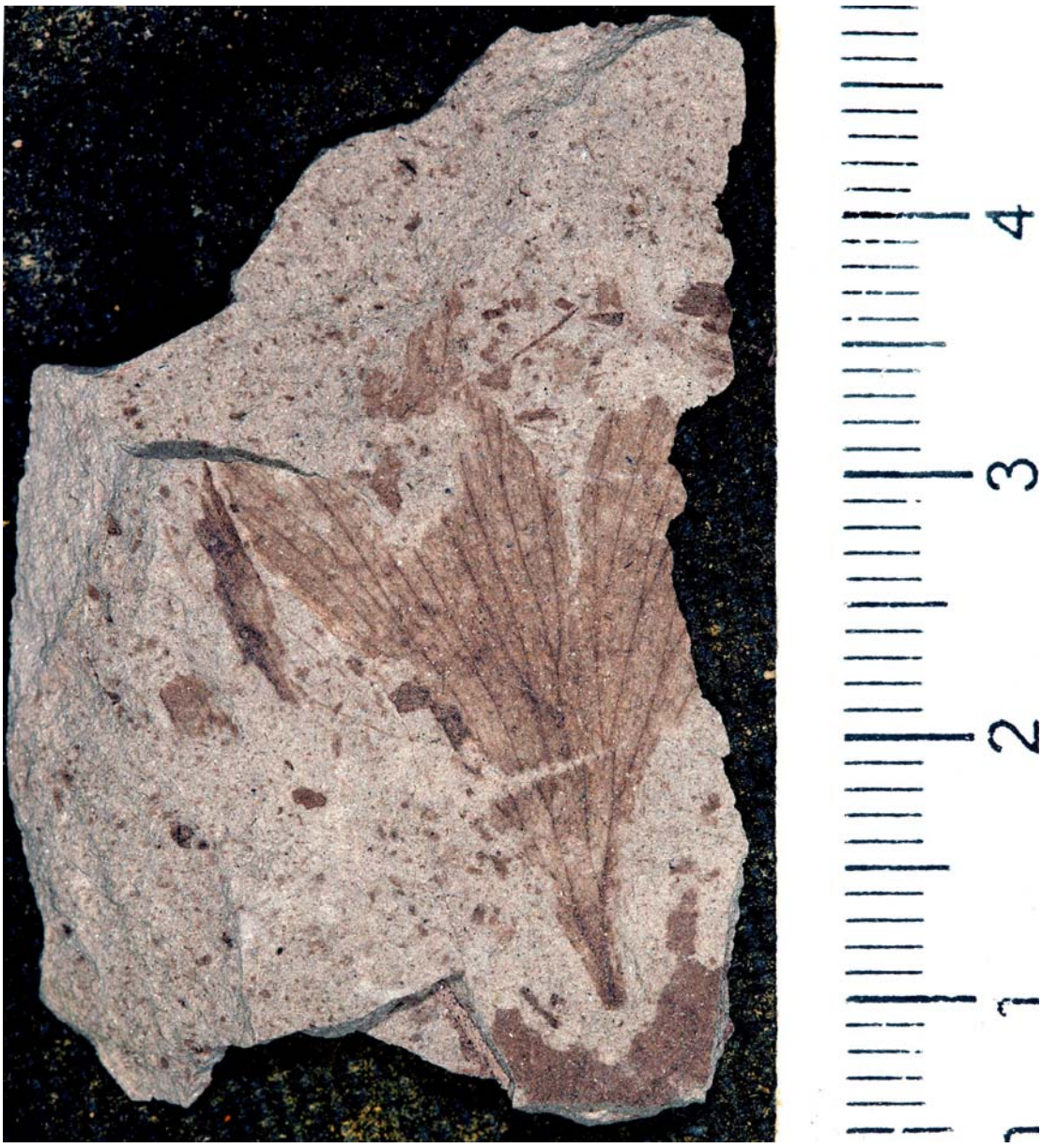


Morphotype CVA2, USNM 554664
Description: Leaf compound, marginal petiolate. Laminar size notophyll, L:W ratio 1.2:1, shape complex. Margin palmately and pinnately lobed, Apex acute, rounded, symmetrical, base obtuse, lobate, symmetrical.
Primary venation palmate, 3basal veins. Secondary vein framework craspedodromous, minor secondary veins present, secondary vein angle acute, spacing decreasing smoothly toward apex, marginal secondary vein present.
Intercostal tertiary vein fabric irregular reticulate, FEVs not present.
Teeth present only at lobe apices. Sinus shape rounded, tooth shape convex/convex.
Principle vein termination at apical, accessory veins running from sinus, apex cassidate.
Interpretation: likely herbaceous, eudicot (cf. *Ambrosia artemisifolia*)



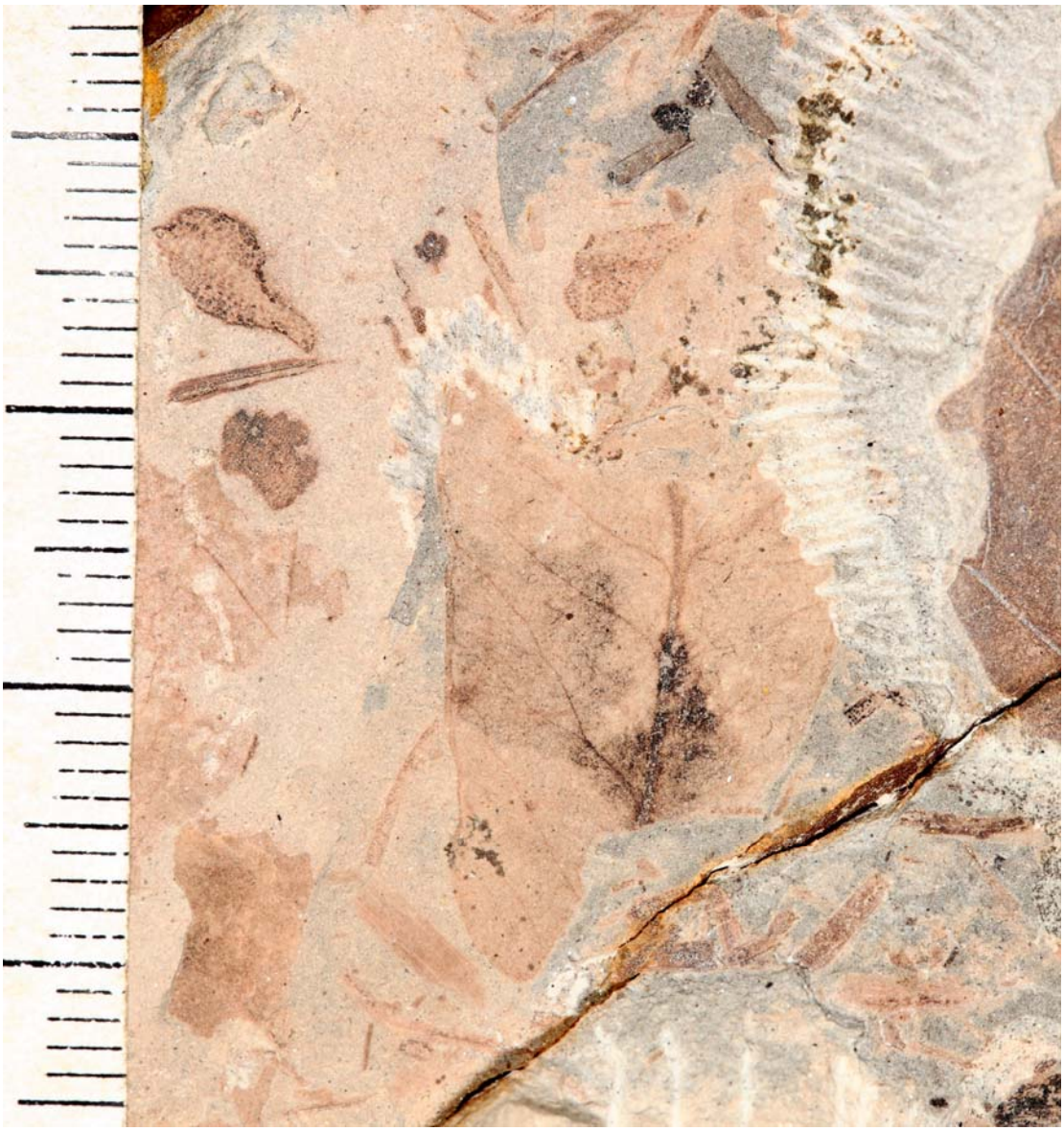
Morphotype CVA3, USNM 554017
Description: Leaf simple, sessile, leaf attachment marginal, buds occasionally visible in the axils of the leaves. Laminar size leptophyll, L:W ratio 1:1, shape flabellate, unlobed. Apex obtuse, rounded; base acute, concave or straight.
Primary vein framework dichotomous; 1 basal vein, primary veins irregular dichotomous, terminate at margin. One order of minor veins sometimes present; intercostal tertiary vein fabric not present or irregular reticulate. FEVs not present. Distal margin serrate, tooth spacing variable, 5-9 teeth per centimeter, sinuses rounded, teeth minute, principle vein termination at apex of tooth, accessory veins absent, tooth apex simple.
Interpretation: likely herbaceous, affinity unknown (cf. *Circaeaster*)

Morphotype CVA5, USNM 554083
Description: Herbaceous shoots, leaves axillary. Leaf simple, sessile. Laminar size nanophyll, L:W ratio 1:1, flabellate, lobed, distal margin serrate. Apex obtuse, rounded, symmetrical; base acute, concave or straight, symmetrical.
Primary venation dichotomous; 1 basal vein. Secondary vein framework absent. Minor veins absent. FEVs absent.
Tooth spacing variable, 5-9 teeth per centimeter, sinuses rounded. Principle vein termination at apex of tooth, accessory veins absent, tooth apex simple.
Interpretation: likely herbaceous

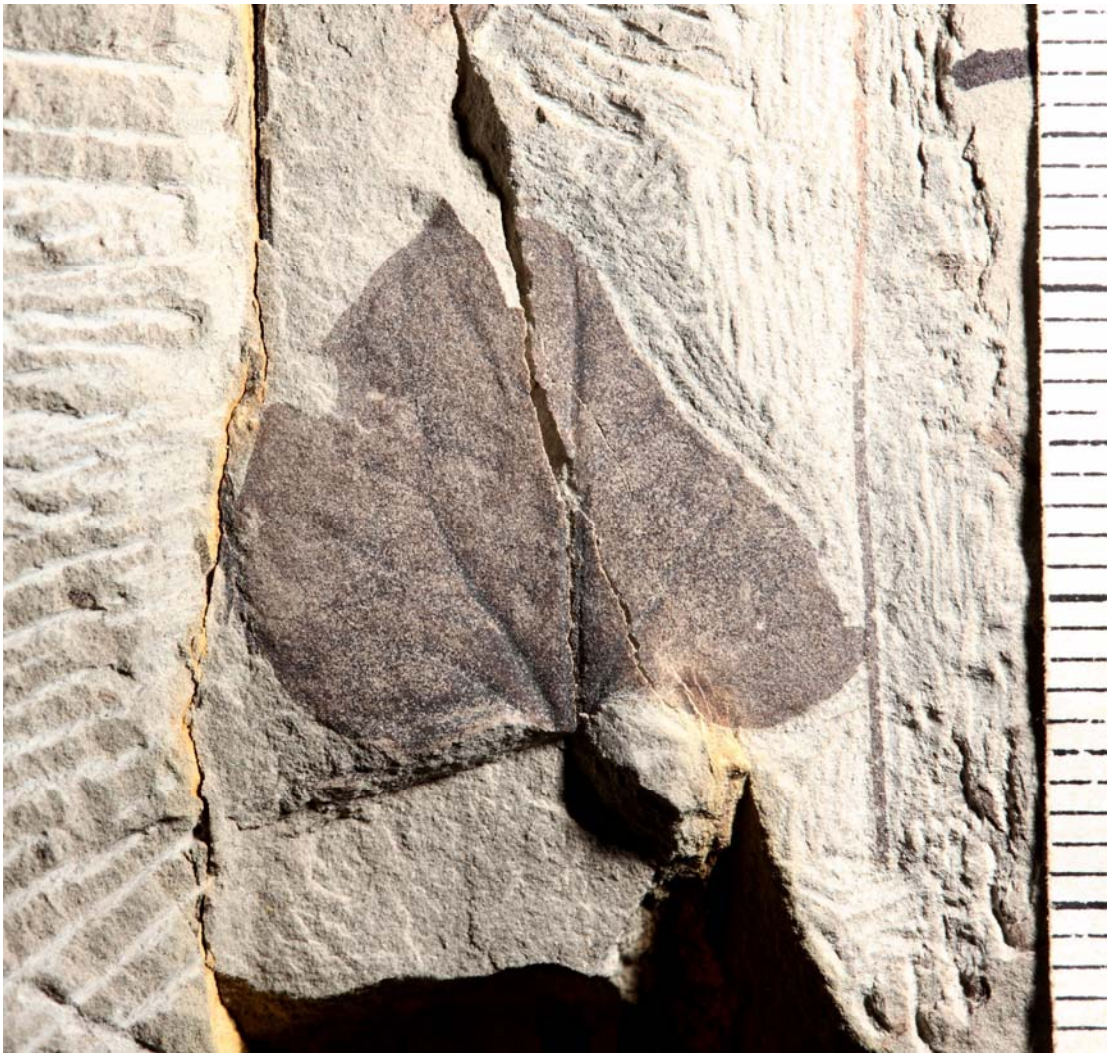


Morphotype CVA6, USNM 553964
Description: Leaf simple, marginal petiolate. Laminar size mesophyll, L:W ratio unknown, shape unknown. Margin pinnately lobed, serrate, apex unknown, base obtuse to reflex, lobate, asymmetrical.
Primary vein framework pinnate, number of basal veins 1. Secondary vein framework craspedodromous. Interior secondary veins present, minor secondary veins craspedodromous. Secondary vein angle acute, spacing irregular. Intercostal tertiary vein fabric irregular reticulate, epimedial tertiaries reticulate. Quaternary vein fabric irregular reticulate, FEVs not observed.
Tooth spacing irregular, two orders of teeth. Sinus shape angular, tooth shape convex/convex. Principle vein termination apical, accessory veins running from sinus, tooth apex simple.
Interpretation: likely shrub, eudicot

Morphotype CVA7, USNM 553836
Description: Leaf organization unknown, petiole unknown. Laminar size leptophyll, L:W unknown, shape likely elliptical. Margin entire (unlobed and untoothed). Apex unknown, base unknown.
Primary vein framework pinnate. Secondary vein framework craspedodromous, attachment decurrent, angle acute, occasionally dichotomous, spacing irregular, intramarginal secondary present. Intercostal tertiary vein fabric irregular reticulate. FEVs not observed.
Tooth spacing irregular, multiple orders of teeth (≥2). Sinus shape angular, tooth shape convex/convex, principle vein termination apical, accessory veins running from sinus, tooth apex simple
Interpretation: habit unknown, non-monocot

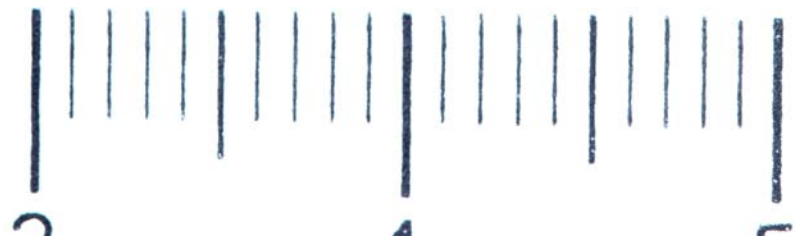


Morphotype CVA8, USNM 553841
Description: Leaf simple, marginal petiolate. Laminar size leptophyll, L:W ratio unknown, shape ovate. Margin entire. Apex unknown, likely acute; base reflex, cordate, symmetrical.
Primary vein framework palmate, 5 basal veins. Secondary vein framework festooned brochidodromous, minor secondary veins brochidodromous. tertiary veins not preserved.
Interpretation: likely shrub or liana, non-monocot

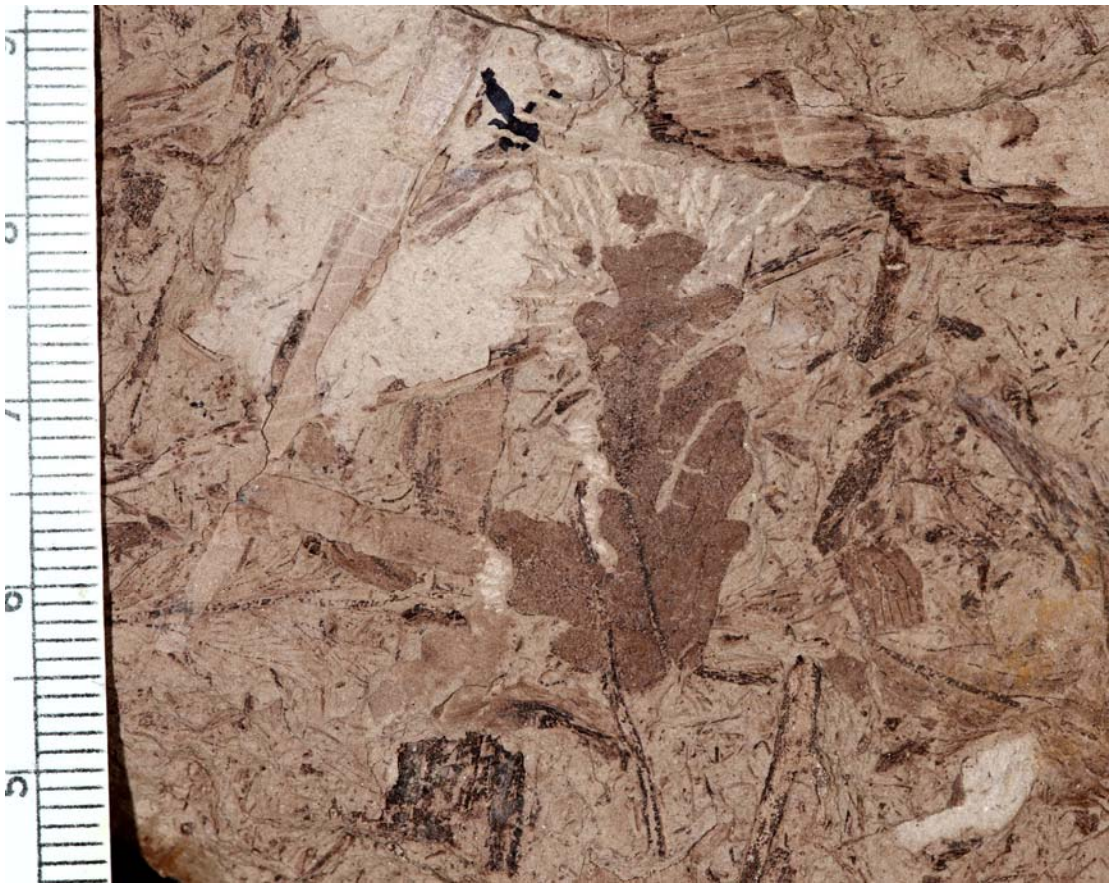


Morphotype CVA9, USNM 554701
Description: Leaf compound, marginal petiolate. Laminar size unknown, L:W ratio unknown, lamina shape unknown. Margin untoothed, at least twice pinnately lobed. Apex acute, rounded symmetrical, base unknown.
Primary vein framework pinnate. Secondary vein framework mixed craspedodromous and semicraspedodromous, minor secondary veins craspedodromous, secondary vein spacing decreases distally, angle acute, marginal secondary vein present. Intercostal tertiary vein fabric irregular reticulate, FEVs not observed.
Teeth only at lobe apices. Sinus shape rounded, tooth shape convex/convex. Principle vein termination marginal, accessory veins running from sinus, tooth apex cassidate.
Interpretation: herbaceous, eudicot

Morphotype CVA11, USNM 553866
Description: Leaf simple, centrally peltate. Laminar size nanophyll, L:W ratio 1:1, laminar shape elliptic. Margin entire, apex obtuse, rounded symmetrical; base obtuse, rounded, symmetrical.
Primary vein framework actinodromous, 5-7 basal veins. Secondary vein framework festooned brochidodromous, secondary vein spacing decreases distally. Intercostal tertiary vein fabric irregular reticulate, FEVs absent.
Interpretation: aquatic herb, Nymphaeales



Morphotype CVA12, USNM 553930
Description: Leaf compound, marginal petiolate. Laminar size nanophyll, L:W ratio 2:1, shape unknown. Margin untoothed, pinnately lobed. Apex unknown, base shape obtuse, rounded, symmetrical.
Primary venation pinnate. Secondary vein framework craspedodromous, agrophic veins present, minor secondary veins mixed semicraspedodromous and craspedodromous, secondary vein spacing decreasing toward apex, angle acute, marginal secondary vein present. Intercostal tertiary vein fabric irregular reticulate, FEVs not visible.
Teeth only at lobe apices. Sinus shape rounded, tooth shape convex/convex. Principle vein termination marginal, accessory veins running from sinus, tooth apex cassidate
Interpretation: herbaceous, eudicot



Morphotype CVA13, USNM 553982
Description: Leaf organization unknown. Laminar size, shape unknown. Margin entire. Apex and base unknown.
Primary vein framework apparently pinnate. Secondary vein framework brochidodromous, secondary vein spacing irregular, angle acute. Intercostal tertiary vein fabric alternate percurrent, epimedial tertiaries reticulate, Quaternary veins irregular reticulate, FEVs not observed.
Margin lobed, teeth only at lobe apices. Tooth spacing decreasing toward apex. Sinus shape rounded, tooth shape CV/CV, principle vein termination marginal, accessory veins running from sinus, tooth apex cassidate.

Morphotype CVA14, USNM 554003
Description: Leaf simple, centrally peltate. Laminar size microphyll, L:W ratio unknown, laminar shape elliptical? Margin serrate, unlobed. Apex, base not visible. Primary vein framework palmate. Secondary vein framework festooned semicraspedodromous. Intercostal tertiary vein fabric regular reticulate. FEVs not visible.
Tooth spacing irregular, one order of teeth. Sinus shape rounded, tooth shape convex/convex. Principle vein termination apical, accessory veins running from sinus, tooth apex cassidate.
Interpretation: aquatic herb, Nelumbonaceae

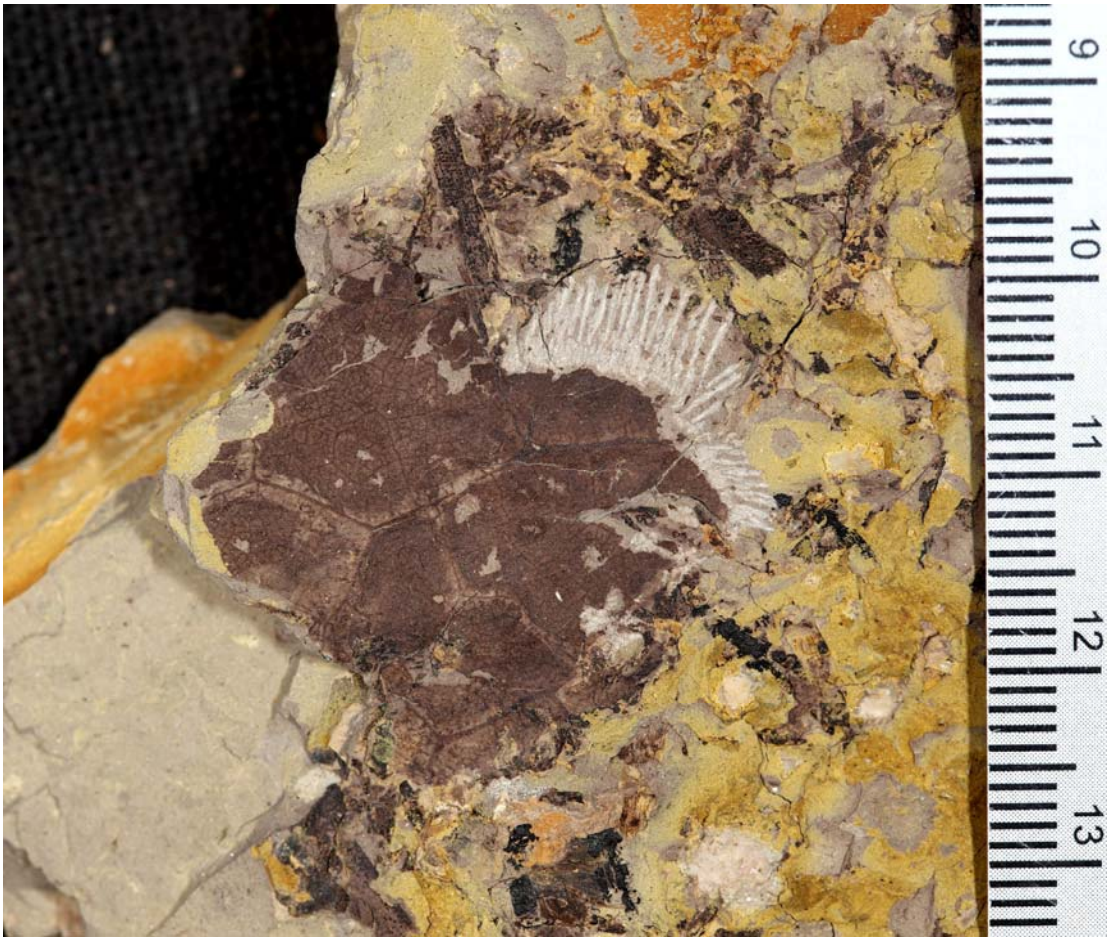
Morphotype CVA17, USNM 554018
Description: Leaf simple, marginal petiolate. Laminar size nanophyll, L:W ratio 1:1.5, laminar shape elliptic. Margin, unlobed, serrate. Apex rounded, obtuse, symmetrical, base truncate, 180°.
Primary vein framework palmate, 5? basal veins. Secondary vein framework craspedodromous. Intercostal tertiary vein fabric irregular reticulate, FEVs not visible.
Tooth spacing irregular, two orders of teeth. Sinus shape rounded, tooth shape convex/convex. Principle vein termination marginal.
Interpretation: herbaceous, angiosperm

Morphotype CVA18, USNM 554049
Description: Leaf organization unknown, petiole unknown. Laminar size microphyll, shape unknown. Margin unknown. Apex and base unknown.
Primary venation pinnate. Secondary vein framework looped (brochidodromous or semicraspedodromous), secondary vein attachment decurrent, angle acute, spacing irregular. Intercostal tertiary vein fabric irregular reticulate, epimedial tertiaries reticulate. FEVs not visible.

Morphotype CVA19, USNM
Description: Leaf simple, marginal petiolate. Laminar size, L:W ratio unknown, shape unknown. Margin at least twice pinnately lobed. Apex shape acute, rounded, symmetrical, base lobate, reflex, symmetrical.
Primary vein framework pinnate. Secondary vein framework craspedodromous, angle acute, spacing decreasing toward apex, minor secondary veins craspedodromous, marginal secondary vein present. Intercostal tertiary vein fabric irregular reticulate, FEVs not visible.
Teeth only at lobe apices. Sinus shape rounded, tooth shape CV/CV. Principle vein termination at apex, accessory veins running from sinus, tooth apex cassidate.
Interpretation: herbaceous, eudicot

Morphotype CVA20 USNM 554117
Description: Leaf simple petiolate. Laminar size microphyll, L:W ratio 9:7, laminar shape ovate. Margin serrate, pinnately lobed. Apex straight, acute, symmetrical, base concave, obtuse, symmetrical. Lamina covered in minute, red, translucent resin bodies.
Primary vein framework pinnate. Secondary vein framework craspedodromous. Secondary vein angle acute, spacing decreasing toward apex; interior minor secondary veins craspedodromous, marginal secondary vein present. Intercostal tertiary vein fabric irregular reticulate, epimedial tertiarties reticulate. FEVs not visible.
Tooth spacing variable, two orders of teeth. Sinus shape rounded, tooth shape convex/convex. Principle vein termination marginal, accessory veins running from sinus, tooth apex cassidate.
Interpretation: herbaceous, eudicot

Morphotype CVA21, USNM 554150
Description: Leaf organization unknown, petiole unknown. Laminar size, shape unknown. Margin unknown. Apex and base unknown.
Primary vein framework unknown. Secondary vein framework looped. Intercostal tertiary vein fabric regular reticulate. Quaternary vein fabric irregular reticulate, FEVs not visible.

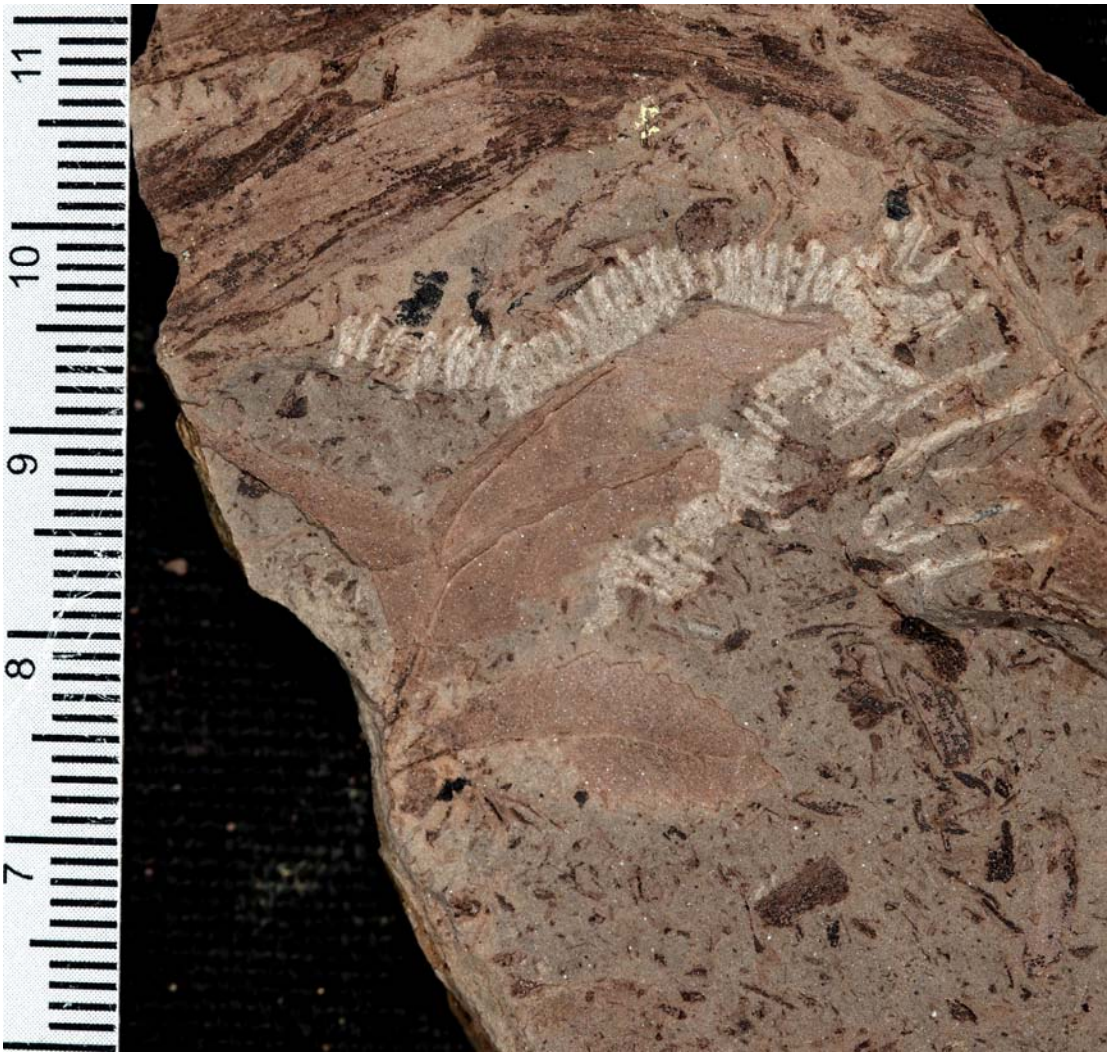


Morphotype CVA22, USNM 554156
Description: Leaf pinnately compound, marginal petiolate, distal portion of rachis winged. Laminar size notophyll, L:W ratio unknown, shape unknown. Margin serrate unlobed, terminal leaflet serrate and lobed. Apex unknown, leaflet bases acute, pinnatisect, asymmetrical.
Primary vein framework, pinnate. Secondary vein framework mixed brochidodromous and semicraspedodromous. Secondary vein angle acute, spacing irregular. Intercostal tertiary vein fabric irregular reticulate, exterior tertiary course looped. FEVs not visible.
Tooth spacing unknown. Sinus shape rounded, tooth shape convex/convex, principle vein termination marginal, accessory veins running from sinus, tooth apex unknown.
Interpretation: Shrub, eudicot (cf. *Sapindopsis* Fontaine emend. Golovneva, 2005)

Morphotype CVA23, USNM 554393
Description: Leaf compound, marginal petiolate. Laminar size nanophyll, L:W ratio >1:1, shape elliptic, asymmetrical. Margin serrate, unlobed. Apex acute, base unknown.
Primary vein framework pinnate. Secondary vein framework craspedodromous. Secondary vein angle acute, spacing irregular. Intercostal tertiary vein fabric irregular reticulate. FEVs not visible.
Tooth spacing irregular, 1-2 per cm. Sinus shape acute, tooth shape convex/straight, principle vein termination marginal.

Morphotype CVA24, 554425 (10+)
Description: Leaf pinnately compound, marginal petiolate, leaflets sessile, rachis winged, leaflet attachment angle acute. Laminar size microphyll, L:W ratio >>1:1. Apex unknown.
Primary vein framework, pinnate. Secondary vein framework brochidodromous. Secondary vein angle acute, spacing irregular, intramarginal secondary vein present. Intercostal tertiary vein fabric irregular reticulate. FEVs not visible.
Interpretation: herbaceous or shrubby, eudicot (cf. *Sapindopsis* Fontaine emend. Golovneva, 2005)

Morphotype CVA25, USNM, 554422
Description: Leaf pinnately compound, marginal petiolate, leaflets sessile, rachis winged, leaflet attachment angle acute. Laminar size microphyll, L:W ratio 3:1. Margin serrate, unlobed. Apex acute, straight, symmetrical.
Primary vein framework, pinnate. Secondary vein framework craspedodromous. Secondary vein angle acute, spacing regular. Intercostal tertiary vein fabric not visible.
Tooth spacing regular, single order, 7 teeth/cm. Sinus shape acute, tooth shape straight/straight. Principle vein termination marginal.
Interpretation: herb or shrub, eudicot (cf. *Sapindopsis* Fontaine emend. Golovneva, 2005)



Morphotype CVA27, USNM 554640
Description: Leaf organization unclear. Marginal petiole. Laminar size microphyll. Margin pinnately lobed; basal lobed pinnatisect, sinus depth decreasing distally. Apex unknown, base obtuse, decurrent. Primary venation pinnate, secondary veins craspedodromous, acute, terminating in teeth at lobe apices.
Interpretation: habit unknown, eudicot.

Morphotype CVA28, USNM 554641
Description: Leaf simple, centrally peltate. Laminar size microphyll, laminar shape unknown. Margin unknown. Apex/base unknown. Leaf areoles appear raised. Primary vein framework palmate, 6 basal veins. Secondary vein framework festooned brochidodromous. Intercostal tertiary vein fabric irregular reticulate, exterior tertiary course looped. FEVs not visible.
Interpretation: Aquatic herb

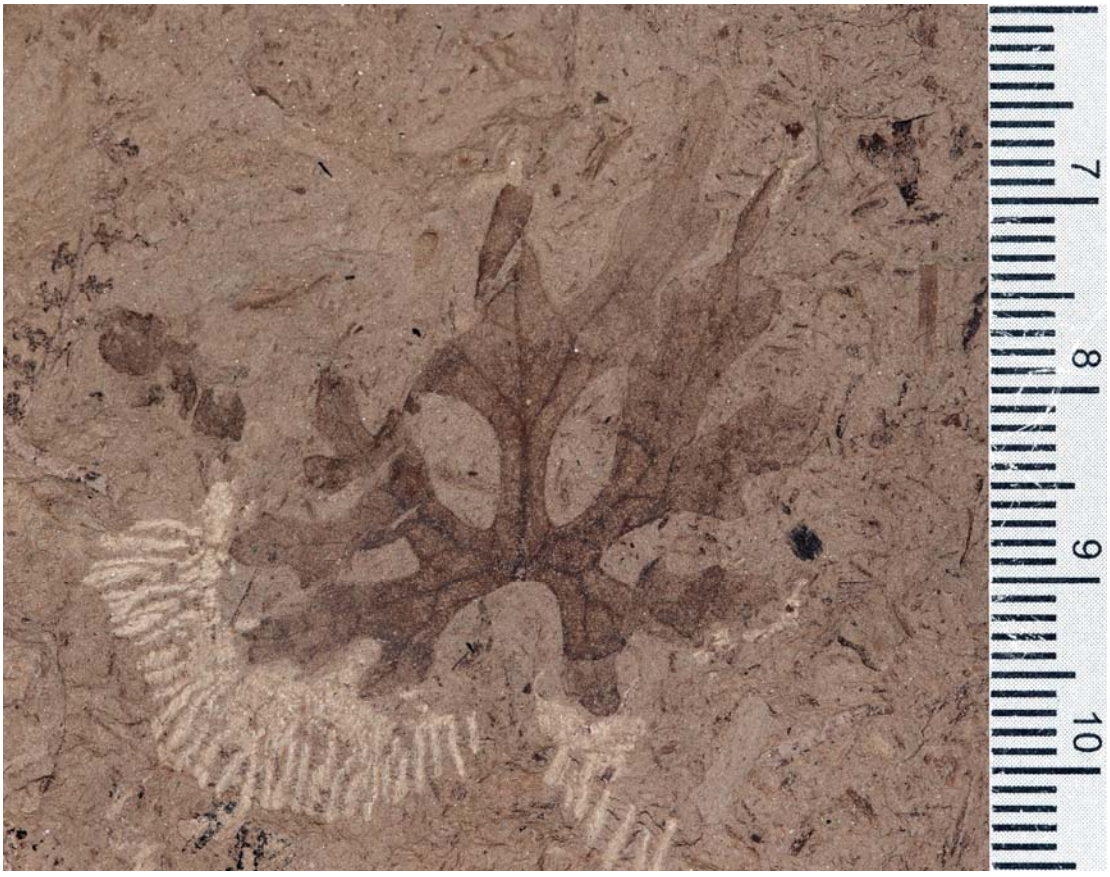
Morphotype CVA29, USNM 554716
Description: Leaf pinnately compound, marginal petiolate, leaflets sessile, rachis winged, leaflet attachment angle acute. Laminar size notophyll, L:W ratio >>1:1. Apex unknown, base strongly asymmetrical.
Primary vein framework, pinnate. Secondary vein framework brochidodromous. Secondary vein angle acute, spacing irregular, intramarginal secondary vein present. Intercostal tertiary vein fabric irregular reticulate. FEVs not visible.
Interpretation: herbaceous or shrubby, eudicot (cf. *Sapindopsis* Fontaine emend. Golovneva, 2005)

Morphotype CVA30, USNM 554661
Description: Leaf compound, marginal petiolate. Laminar size microphyll, laminar shape unknown. Margin lobed. Apex unknown, base acute, asymmetrical.
Primary vein framework pinnate. Secondary vein framework craspedodromous. Secondary vein angle acute, spacing decreasing toward apex; marginal secondary vein present. Intercostal tertiary vein fabric not visible.
Teeth only at lobe apices. Sinus shape rounded, tooth shape convex/convex. Principle vein termination marginal, accessory veins running from sinus, tooth apex cassidate.
Interpretation: herbaceous eudicot

Morphotype CVA32, USNM 554700
Description: Leaf simple, marginal petiolate. Laminar size microphyll, laminar shape ovate. Margin serrate, unlobed. Apex acute, rounded, base acute, concave, asymmetrical.
Primary vein framework pinnate. Secondary vein framework craspedodromous. Secondary vein angle acute, spacing regular. Intercostal tertiary vein fabric not visible.
Teeth spacing regular, one order, 6-7 teeth/cm. Sinus shape rounded, tooth shape ST/ST, principle vein termination marginal, accessory veins not visible, tooth apex cassidate.

Morphotype CVA33, USNM 554683
Description: Leaf compound, petiole insertion marginal. Laminar size unknown, shape unknown. Margin lobed, Apex, base unknown. At least five leaflets, leaflets deeply lobed.
Primary vein framework unknown. Secondary vein framework craspedodromous. Secondary vein angle acute, minor secondary veins craspedodromous.
Teeth only at lobe apices. Sinus shape rounded, tooth shape convex/convex. Principle vein termination marginal, accessory veins running from sinus, tooth apex cassidate.
Interpretation: herbaceous, eudicot

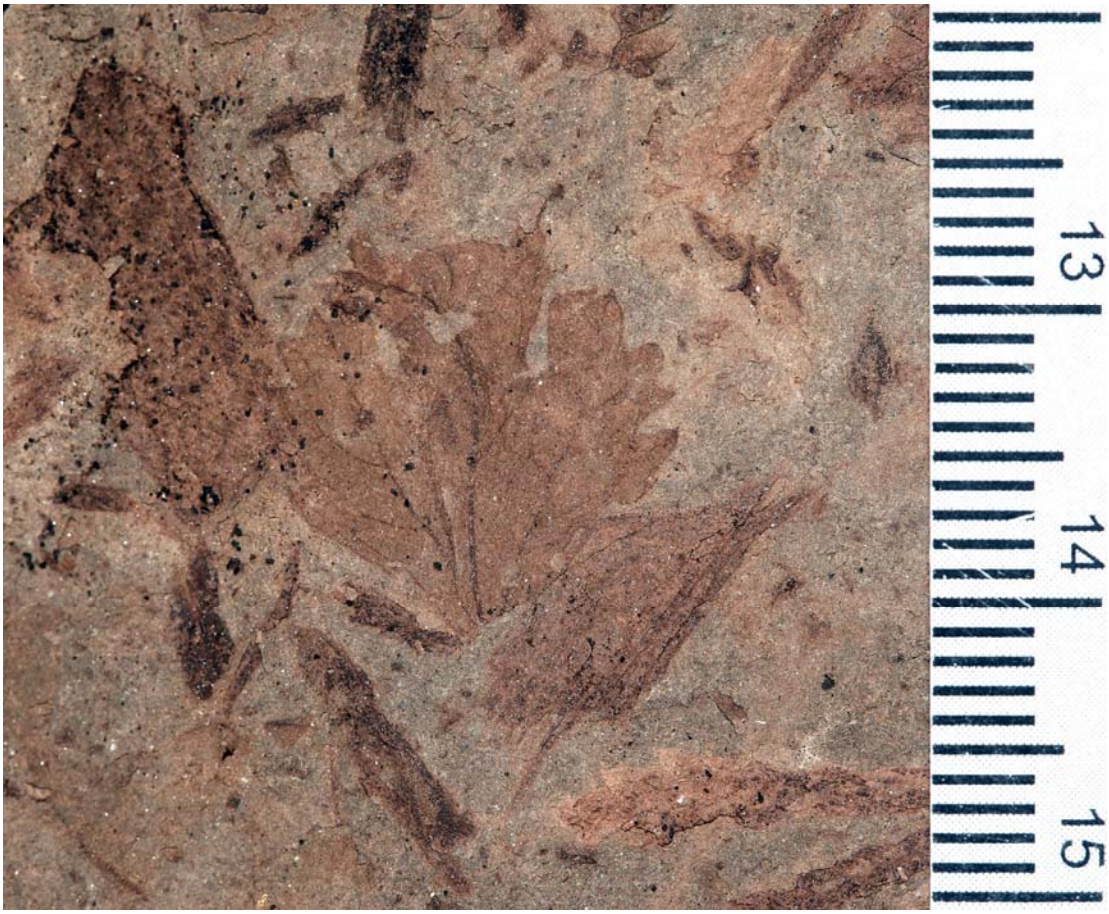
Morphotype CVA34, USNM 554694
Description: Leaf simple, marginal petiolate, petiole orientation perpendicular. Laminar size microphyll, L:W ratio unknown, laminar shape ovate. Margin palmately and pinnately lobed (pedate). Apex shape unknown, base reflex, lobate.
Primary vein framework palmate, 5 basal veins. Secondary vein framework mixed craspedodromous. Secondary vein angle acute, spacing decreasing proximally; minor secondary veins craspedodromous, marginal secondary vein present. Intercostal tertiary vein fabric irregular reticulate, FEVs not visible.
Teeth only at lobe apices. Sinus shape rounded, tooth shape convex/convex. Principle vein termination marginal, accessory veins running from sinus, tooth apex cassidate.
Interpretation: herbaceous, eudicot



Morphotype CVA35, USNM 554768
Description: Leaf organization unknown, petiole unknown. Laminar size microphyll, L:W ratio >1:1, laminar shape elliptic, asymmetrical. Margin serrate, unlobed. Apex acute symmetrical, straight, base acute.
Primary vein framework pinnate. Secondary vein framework craspedodromous. Secondary vein angle acute, spacing irregular. Intercostal tertiary vein fabric not visible.
Tooth spacing irregular, two orders of teeth, ~5/cm. Sinus shape rounded, tooth shape convex/straight, principle vein termination marginal.

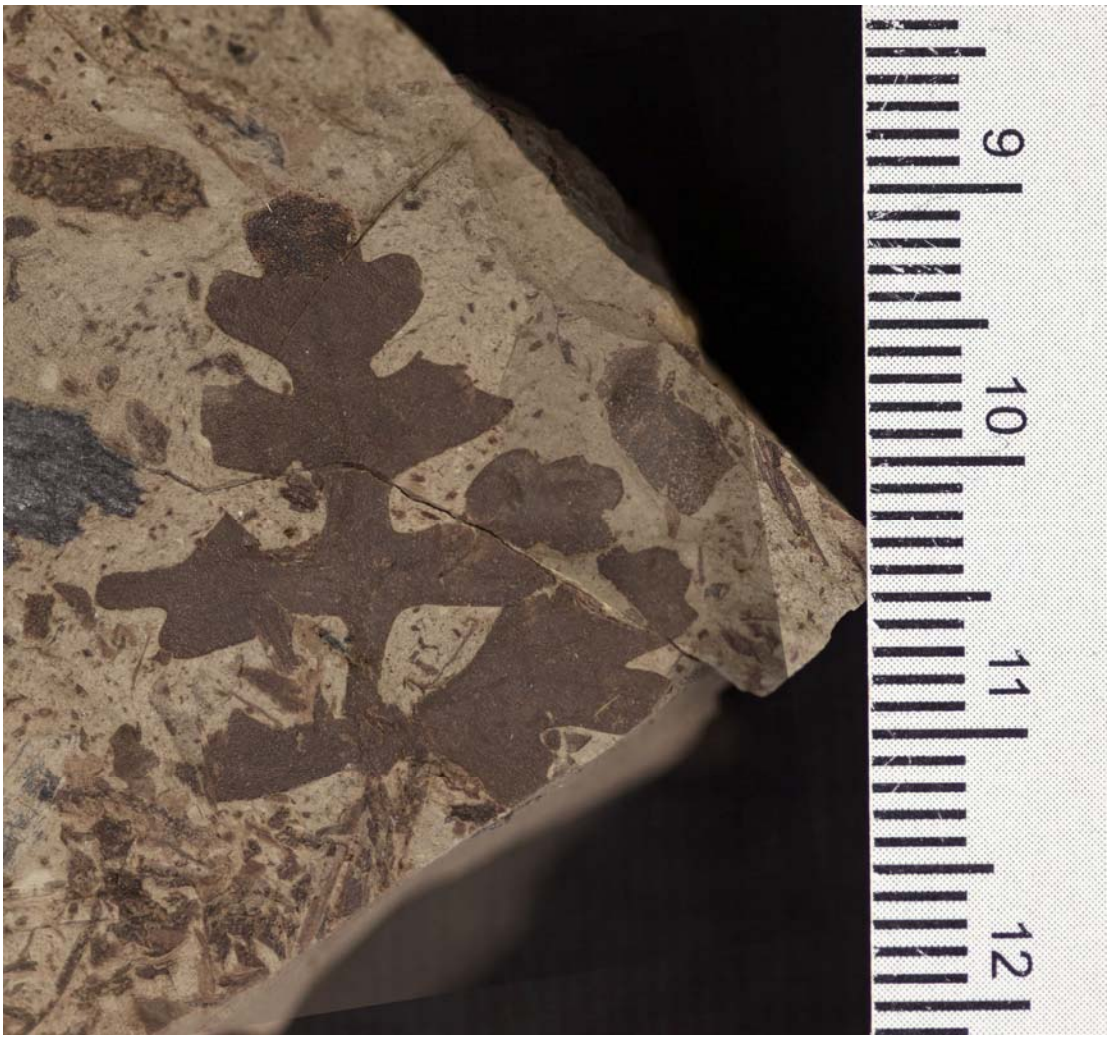
Morphotype CVA36, USNM 554808
Description: Leaf organization unknown, petiole unknown. Laminar size mesophyll, shape unknown. Margin untoothed, palmately lobed. Apex, base unknown.
Primary vein framework palmate ≥5 basal veins. Secondary vein framework unknown. Intercostal tertiary vein fabric unknown.
Teeth at lobe apices only. Sinus shape rounded, tooth shape straight/straight, principle vein termination unknown.

Morphotype CVA37, USNM 554811
Description: Leaf organization unknown, petiole unknown (likely marginal). Laminar size nanophyll, L:W ratio unknown., laminar shape ovate. Margin palmately and pinnately lobed, serrate. Apex acute, base acute.
Primary vein framework palmate, 3 basal veins. Secondary vein framework mixed craspedodromous and semicraspedodromous. Secondary vein angle acute, spacing decreases toward apex; minor secondary veins mixed semicraspedodromous and craspedodromous. marginal secondary vein present. Intercostal tertiary vein fabric irregular reticulate, epimedial tertiarties reticulate. FEVs not visible.
Margin serrate, two orders of teeth. Tooth spacing irregular, decreasing toward apex. Sinus shape rounded, tooth shape convex/convex, principle vein termination marginal, accessory veins running from sinus, tooth apex cassidate.
Interpretation: herbaceous, eudicot

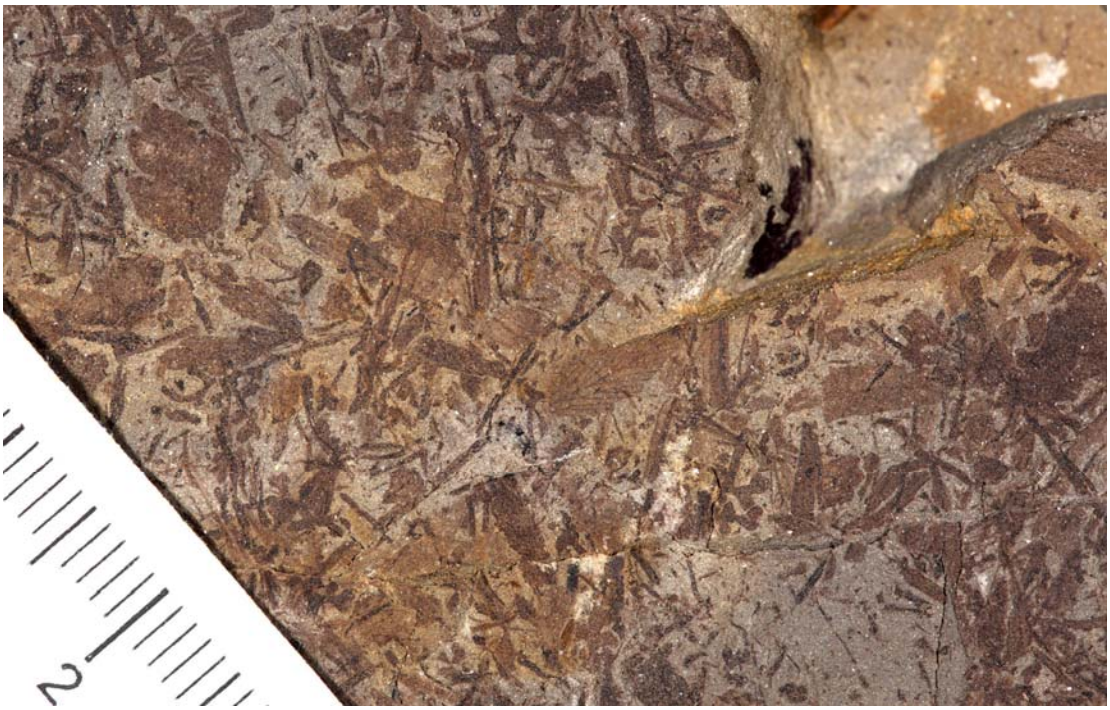


Morphotype CVA39
Description: Leaf pinnately compound, marginal petiolate, rachis winged. Laminar size nanophyll, L:W ratio 2:1, leaflet shape elliptic. Leaflet margin pinnately lobed. Apex acute, rounded, base acute.
Primary vein framework of leaflets pinnate. Secondary vein framework craspedodromous, Secondary vein angle acute, spacing even, marginal secondary vein present. Intercostal tertiary vein fabric not visible.
Teeth only at apices of leaflets and lobes. Spacing regular, 3 per cm. Sinus shape rounded, tooth shape convex/convex. Principle vein termination marginal, accessory veins running from sinus, tooth apex cassidate.
Interpretation: herbaceous, eudicot

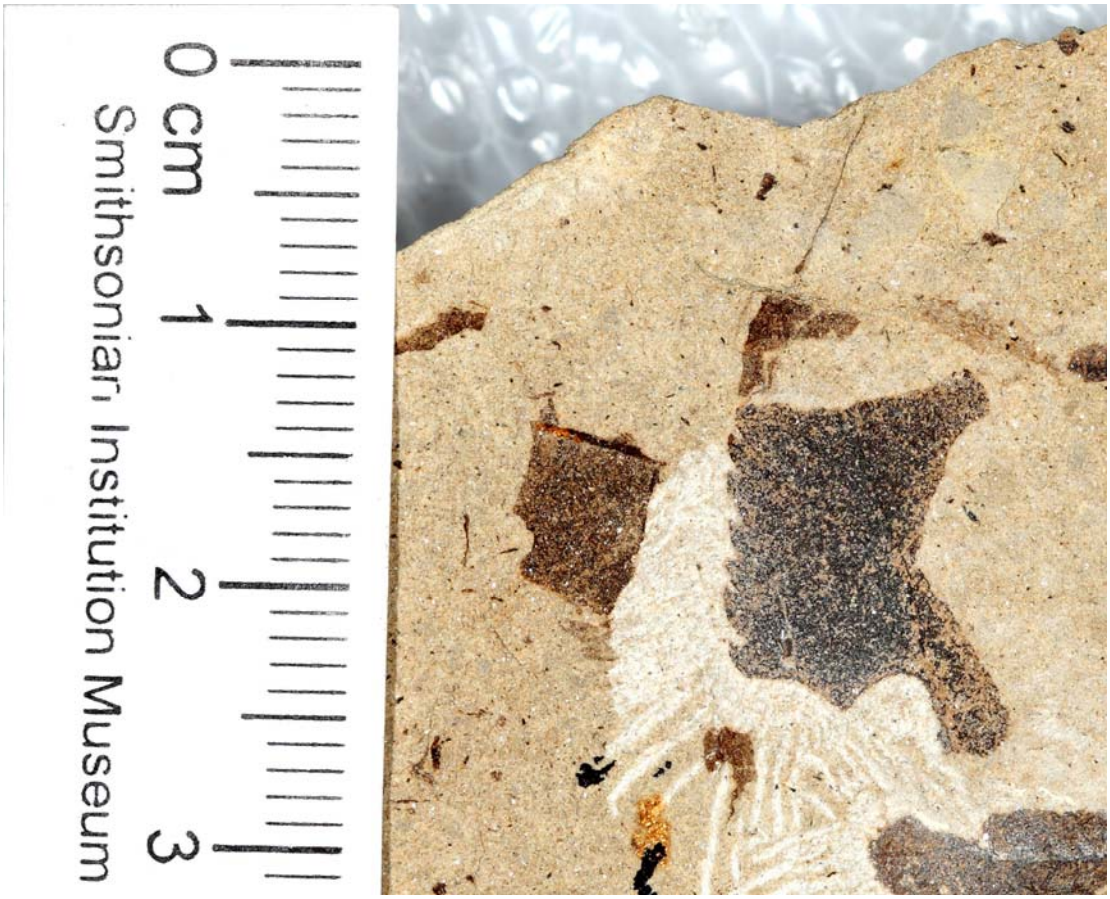
Morphotype CVA40, USNM (NAJ 1212)
Description: Leaf simple, marginal petiolate. Laminar size nanophyll, L:W ratio 2:1, laminar shape ovate. Margin twice pinnately lobed to pedate. Apex obtuse, rounded, base lobate.
Primary vein framework pinnate. Secondary vein framework craspedodromous, Secondary vein angle acute, spacing smoothly decreasing distally; minor secondary veins craspedodromous, marginal secondary vein present. Intercostal tertiary vein fabric not visible.
Teeth only at apices of lobes, spacing regular. Sinus shape rounded, sinus depth smoothly decreases toward apex, tooth shape convex/convex. Principle vein termination marginal, accessory veins running rom sinus, tooth apex cassidate.
Interpretation: herbaceous, eudicot



Morphotype CVA41, USNM 553964
Description: Leaf organization unknown, petiole unknown. Size leptophyll, L:W ratio 1:1, shape elliptic. Margin lobed. Apex obtuse, straight, base unknown.
Venation unknown
Teeth only at lobe apices. Sinuses rounded, tooth shape convex/convex. Principle vein termination marginal, accessory veins running from sinus, tooth apex cassidate.
Interpretation: herbaceous, eudicot



Morphotype CVA42, USNM
Description: Leaf organization unknown, petiole unknown. Size, shape unknown. Margin serrate. Apex, base unknown.
Venation unknown.
Teeth spacing regular, one order of teeth, 7 per cm. sinus shape sharp, acute, tooth shape concave/convex. Principle vein termination marginal, accessory veins not visible, tooth apex simple.
Interpretation: herbaceous, eudicot

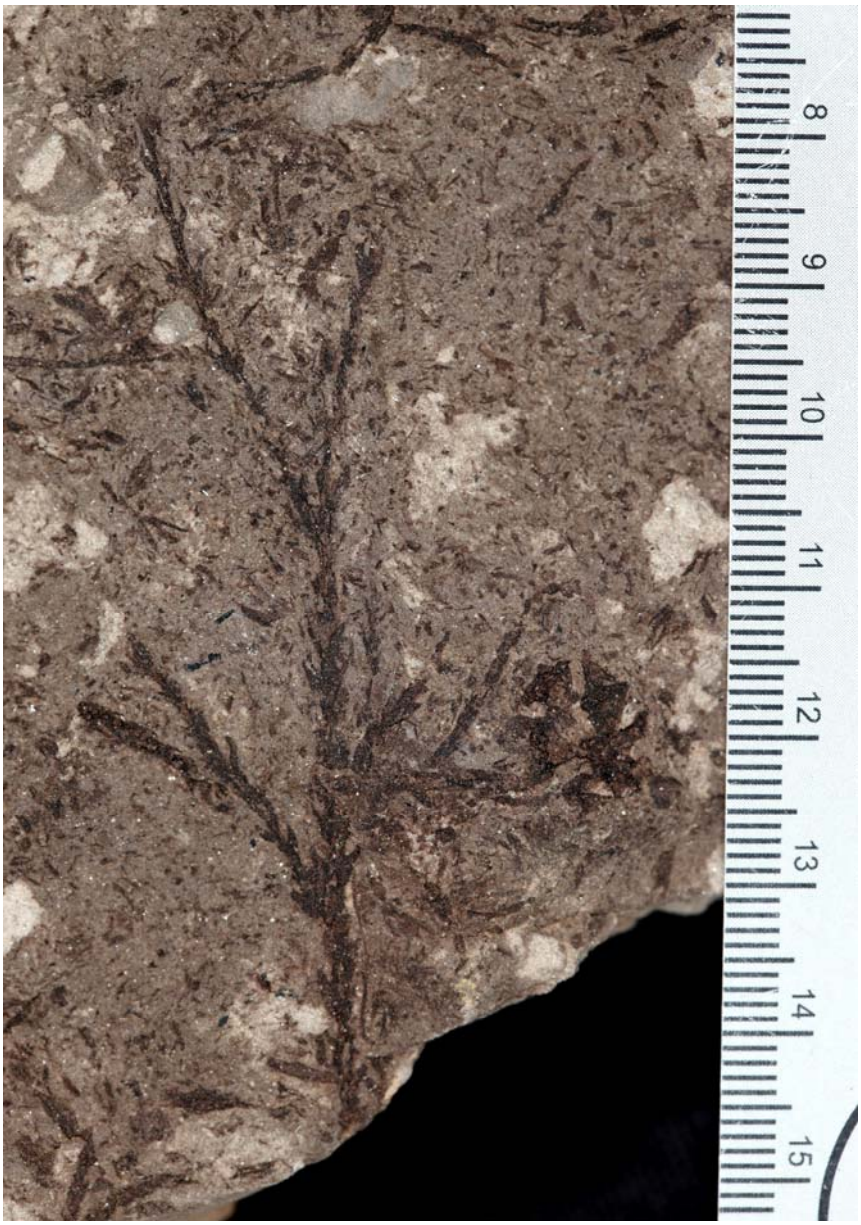


Gymnosperms

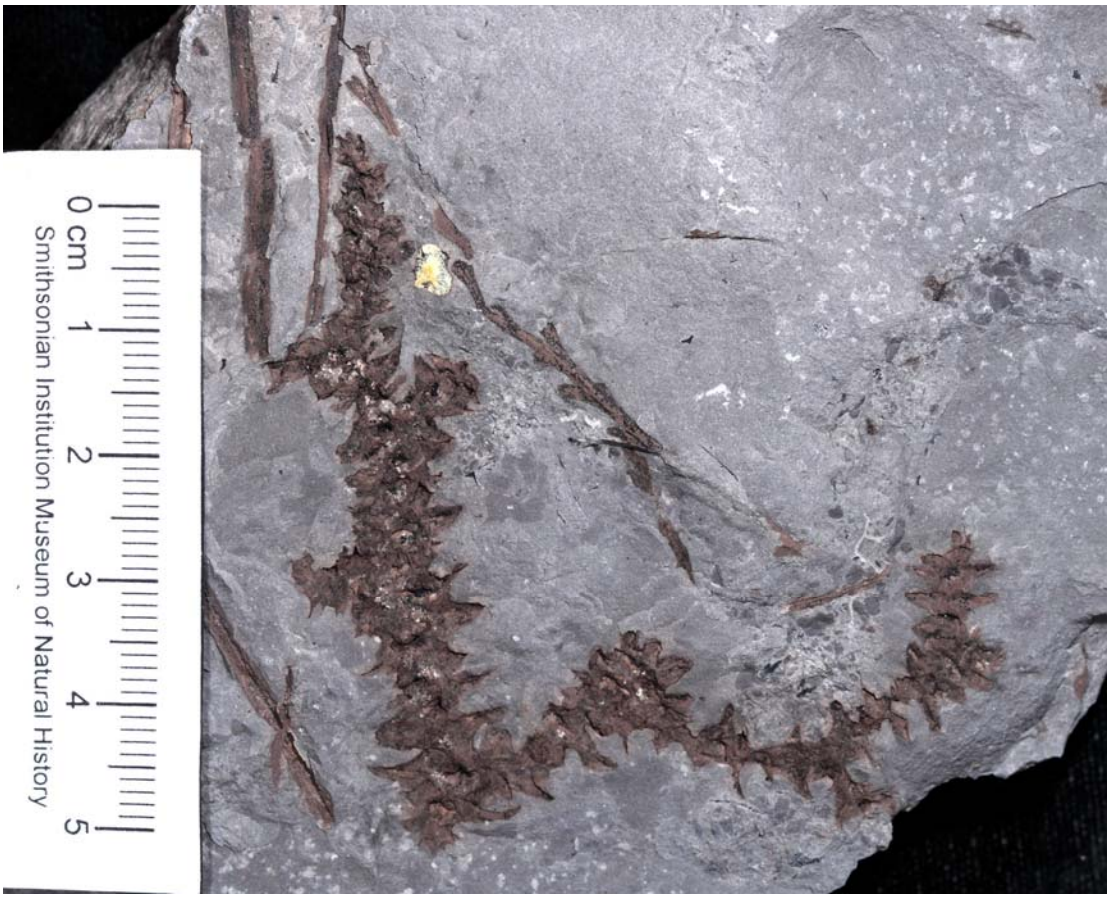
Format of Gymnosperm Descriptions

Shoot architecture, Leaf organization, petiole description, laminar size, length-to-width ratio, shape, lobation, other diagnostic features; Apex angle, shape, description; base angle, shape.
Primary vein framework, description of midvein, secondary vein framework.
Margin, tooth spacing, sinus shape, tooth shape, principle vein, tooth apex description
Description of reproductive structures

Morphotype CVCo1, USNM 553833
Branched conifer shoots with persistent leaves, up to 4mm wide. Branching alternate, irregular, angle of divergence variable acute. Leaves helically arranged, leaf length 1 mm, width 0.5 mm, falcate. Margin entire, unlobed. Apex acute, bases adpressed to the stem forming a cushion.
Venation not observed.
Ovulate cones globose, length 7 to 9 mm, width 6 to 7 mm, attached terminally to axes; cone scales 8 to 10, helically arranged on cone axis, each with a basal stalk and peltate head; basal stalk length 3 mm, width 0.1 to 0.5 mm; head peltate, apex truncate, width 1 to 2 mm. Pollen cones cylindrical, length 5 to 8 mm, width 2 to 4 mm. Pollen sacs attached to abaxial surface of helically arranged, imbricate microsporophylls.



Morphotype CVCo2, USNM 554478
Branched conifer shoots with persistent leaves, up to 1cm wide. Branching irregular, angle of divergence variable. Leaves helically arranged, attached perpendicular to stem, leaf length 4 to 6 mm, width tapering from ~2mm wide, leaf shape falcate. Margin entire, unlobed. Apex acute, base broad, clasping.
Venation not observed.



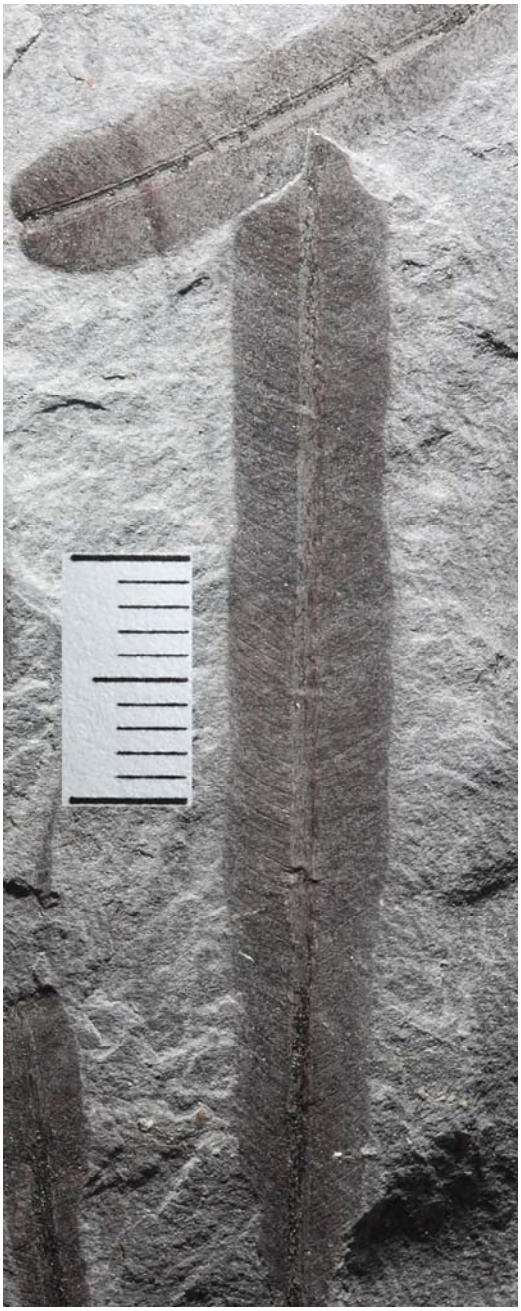
Morphotype CVCo3, USNM 554359
Branched conifer shoots with persistent leaves, up to 4mm wide. Branching alternate, angle of divergence acute. Leaves helically arranged, leaf length 2-3 mm, width 0.5-1 mm, leaves awl shaped. Margin entire, unlobed. Apex acute, base adpressed to the stem forming a cushion.
Venation not observed.

Morphotype CVCo4, USNM 554348
Incomplete conifer shoots with persistent leaves, up to 1.5mm wide. Branching unknown. Leaves helically arranged, leaf length 2mm, awl-shaped, free portion of the leaf 1-1.5mm, width 0.5-1 mm. Margin entire, unlobed. Apex acute, base adpressed to the stem forming a cushion.
Venation not observed.

Morphotype CVCo6, USNM 554362
Leaf simple, lanciolate, falcate, 40mm long, 3mm wide. Apex acute, sharp, unknown. Venation not observed.

Morphotype CVCo7, USNM 554622
Leaf simple, lanciolate, >37mm long, 9mm wide. Margin entire, unlobed. Apex acute, base, acute.
Venation parallel, 14-16 veins in middle of the leaf.

Morphotype CVCy1, USNM 553910
Leaf simple, marginal petiolate. Laminar size notophyll (mesophyll?), length more than 40 cm, width up to 1.1 cm (typically 0.7 cm), shape lanciolate. Margin untoothed, unlobed, slightly undulate. Apex unknown, base straight, acute, symmetrical. Lamina completely covering the midvein.
Primary vein framework pinnate, midvein 1-1.5mm wide; secondary vein framework craspedodromous, secondary vein attachment excurrent, angle acute, near the margin the secondary veins curve slightly toward apex; secondary vein spacing irregular, 16 veins per mm.



Morphotype CVCy2, USNM 554356
Incomplete pinnately compound leaves. Leaflets pinnatisect, attachment perpendicular to rachis, leaflet shape lanciolate. Length 10mm, width up to 1-1.5mm. Margin entire, parallel. Apex truncate. Leaflet attachment adaxial surface of the rachis.
Leaflet venation not observed.

Morphotype CVCy3, USNM 554591
Incomplete pinnately compound leaves. Leaflets pinnatisect, attachment perpendicular to rachis, leaflet shape lanciolate, margins parallel, length 7mm, width up to 1-1.5mm; Margin entire. Apex acute. Leaflet attachment adaxial surface of the rachis.
Leaflet venation not observed.

Morphotype CVG1, USNM 554592
Leaves simple, marginal petiolate. Laminar size microphyll, L:W ratio >1:1, shape flabellate. Margin untoothed, lobed. Apex reflex, straight, symmetrical, base acute, straight, symmetrical.
Primary venation dichotomous.

Morphotype CVG2, (NAJ 1212)
Leaves simple, marginal petiolate. Laminar size notophyll (mesophyll?), L:W ratio <1:1, shape flabellate. Margin untoothed, lobed. Apex reflex, straight, symmetrical, base acute, straight, symmetrical.
Primary venation dichotomous.

Ferns

Format of Fern descriptions

Morphotype code, USNM number
Description: Frond (fragment) organization.
Pinna arrangement, angle, attachment,
Pinnule arrangement, angle, attachment. Pinnule shape, length, width, apex base.
Margin description. Venation open or reticulate. Primary venation, secondary veins, arrangement, angle simple/bifurcating, course.
Fertile morphology. Sori shape, indusium, position; sporangia per sorus

Morphotype CVF1, USNM 554002
Description: Dispersed pinnae once pinnate. Pinnules subopposite to alternate, ascending, decurrent. Pinnule shape ovate, length up to 4mm, width up to 3mm; apex acute, straight, symmetrical; base acute, basiscopic margin decurrent. Margin dentate. Venation open.
Fertile pinna once pinnate, sori solitary, round, terminal on non-laminar pinnules
Affinity: *Coniopteris*

Morphotype CVF2, USNM 554071
Description: Frond fragments pinnate pinnatisect. Pinnae opposite, perpendicular, excurrent. Pinnules subopposite, perpendicular, excurrent. Pinnule shape lanciolate, length up to 10mm, width 2mm; apex acute, rounded, symmetrical; base slightly flaring, symmetrical. Margin entire.
Venation open, primary venation pinnate, secondary veins simple, alternate, ascending, straight, terminating at margin.
Affinity: Gleicheniaceae

Morphotype CVF3, USNM 553859
Description: Frond fragments thrice cut, non-laminar. Primary pinnae arrangement unknown, perpendicular, excurrent. Secondary pinnae alternate, perpendicular, excurrent. Rachilla deflected by pinnules. Pinnules alternate, anadromous, inclined, decurrent. Pinnules shape obovate, minute; apex rounded or reflex, often slightly asymmetrical. Margin smooth. Venation open.

Morphotype CVF4, USNM 554061
Frond (fragment) pinnate pinnatisect. Pinnae alternate, perpendicular, excurrent. Pinnules alternate, inclined excurrent. Pinnule shape triangular, almost as wide as long, up to 2mm long; apex rounded; base broadly attached. Margin smooth
Primary venation pinnate, secondary veins acute, alternate, once forked, terminating at margin.
Sori abaxial, up to 5 per pinnule; Sori round, indusium absent, >5 sporangia per sorus
Affinity: Gleicheniaceae

Morphotype CVF5, USNM 554697
Description: Frond at least twice pinnate. Pinnae alternate, ascending, decurrent. Pinnules alternate, ascending, decurrent. Pinnules ovate-lanciolate, length up to 9cm, width 1cm; apex acute, straight; base acute, asymmetrical, basiscopic margin decurrent. Margin toothed.
Venation open. Primary venation pinnate, secondary veins alternate, adpressed, dichotomizing, terminating at margin.
Affinity: *Anemia*

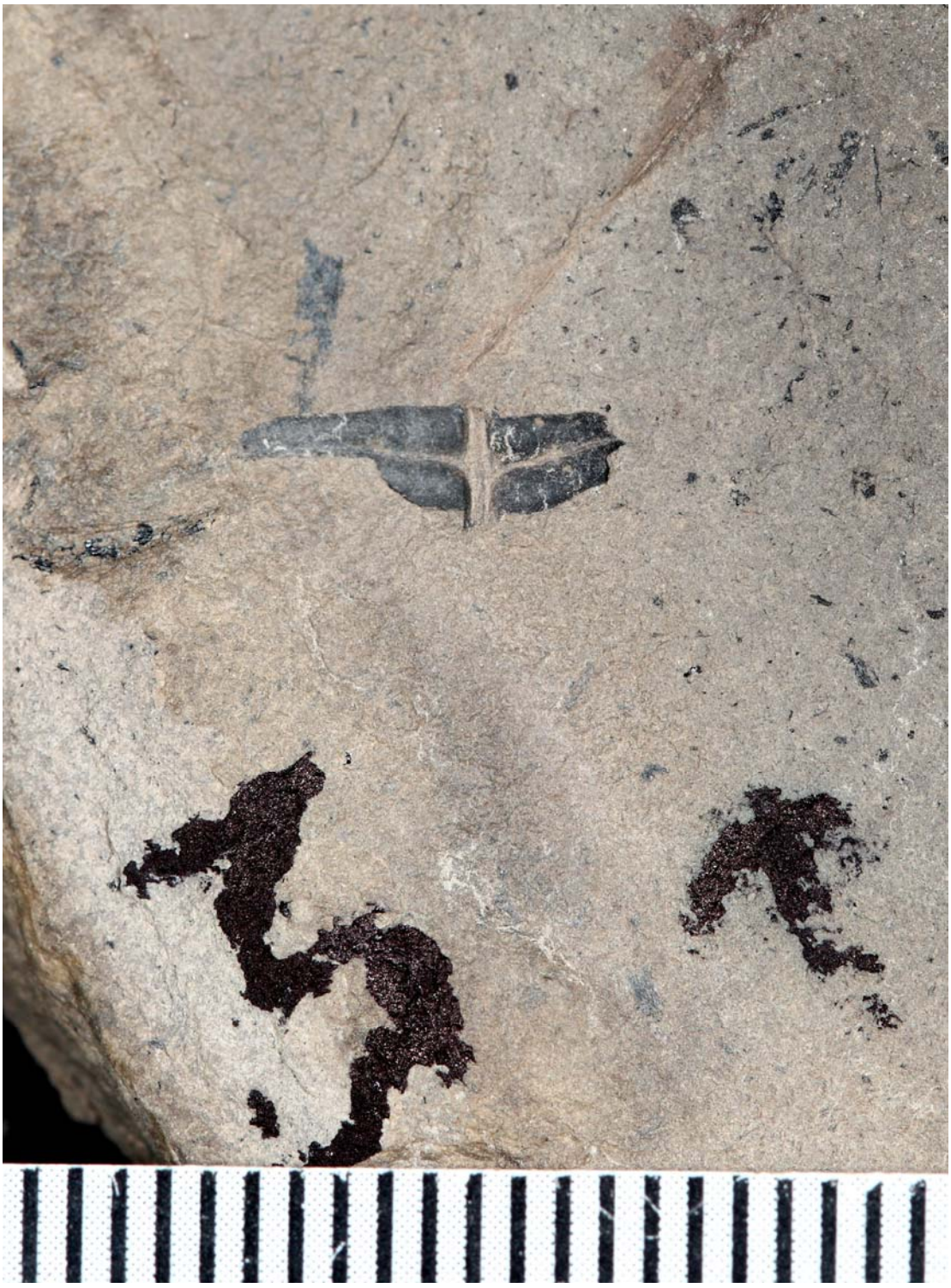
Morphotype CVF6 USNM 554169
Description: Frond pinnate. Pinnules alternate, inclined, decurrent.
Pinnules flabellate, irregularly furcate. Ultimate units narrow (1mm), terminating in two teeth, giving the appearance of a reflex apex. Venation open, dichotomous.
Affinity: *Schizaea*

Morphotype CVF9, USNM 553865
Description: Frond fragment pinnate pinnatisect. Pinna perpendicular, alternate, excurrent. Pinnule shape lanciolate, length 5.2cm, width 4mm. Pinnules subopposite, excurrent, ascending. Pinnule shape narrow; apex rounded, symmetrical; base broadly attached, asymmetrical, basiscopic margin extended down along the rachilla; terminal pinnule elongate, auriculate. Margin entire. Venation open, single midvein.
Affinity: *Pteris*

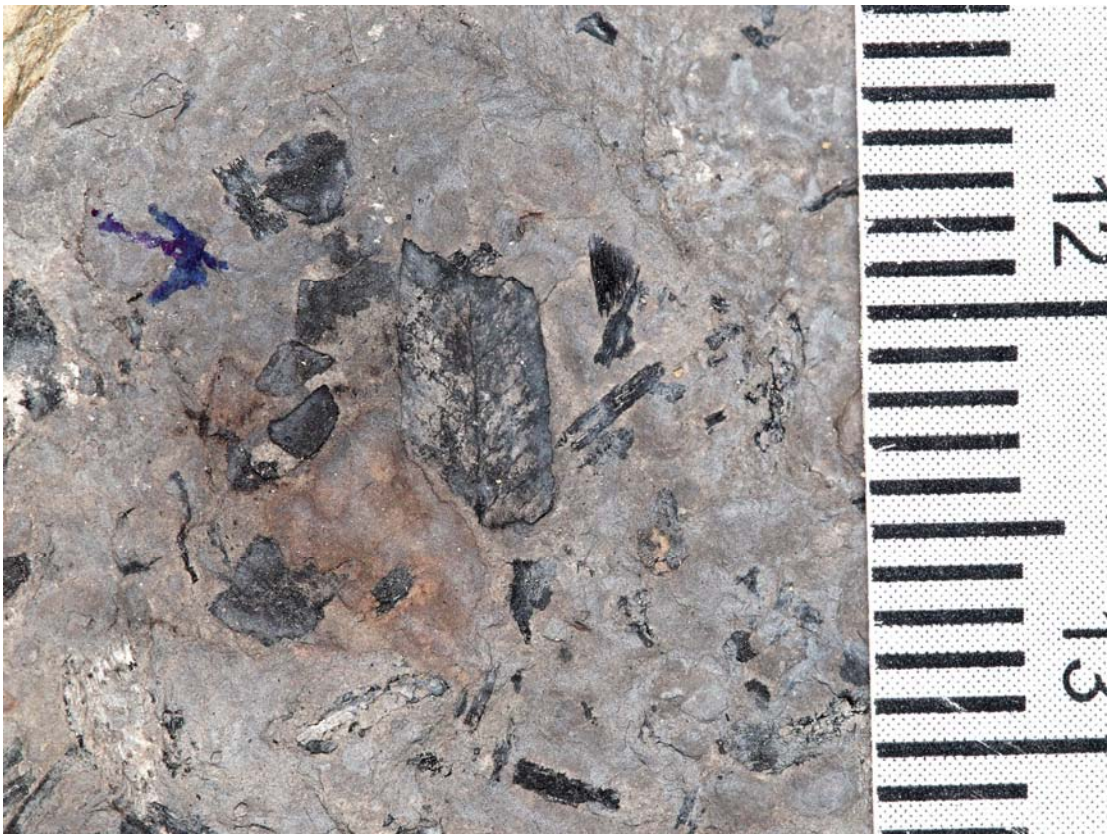
Morphotype CVF10 USNM 553889
Description: Frond fragment pinnate pinnatisect. Pinnae alternate, inclined, excurrent. Pinnule arrangement variable, decurrent, ascending. Pinnule shape ovate and slightly reflex, length 2.5mm, width 2mm; apex rounded; base slightly contracted, basiscopic margin decurrent to rachilla. Margin untoothed. Venation open.

Morphotype CVF11, USNM 554938
Description: Pinna pinnatifid, pinnules deeply dissected, narrow, lobes alternate, adpressed; lobe apices acute, rounded, sinuses narrow, sharp. Margin untoothed. Venation open dichotomous.

Morphotype CVF13, USNM 554468
Description: Frond fragment pinnatisect. Rachilla robust, with central groove. Pinnules opposite, perpendicular, excurrent. Pinnule shape elongate, length 5.5mm long, width 2.5 mm; apex rounded, symmetrical; base broadly attached, symmetrical. Margin untoothed. Venation open, pinnate; midvein distinct.



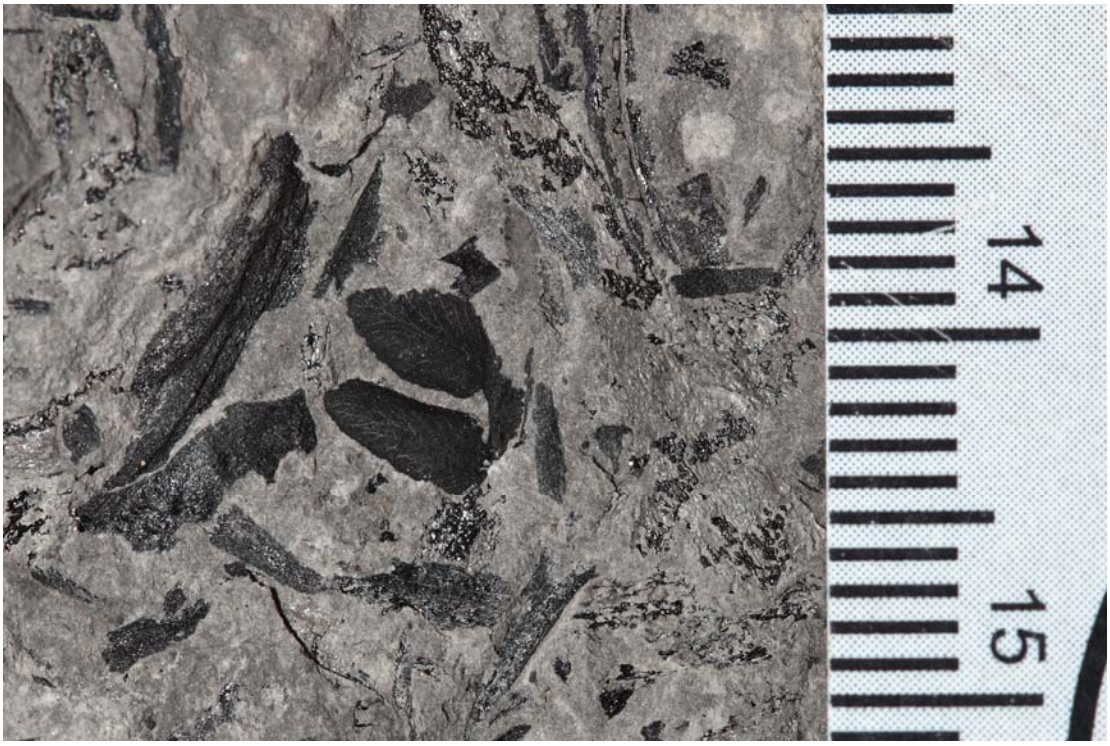
Morphotype CVF14, USNM 554537
Description: Pinnule shape elongate, length >7mm, width 3mm. Margin untoothed. Venation open, pinnate, secondary veins alternate, ascending, once forked, terminating at margin.
Affinity: *Furcillopteris*



Morphotype CVF16, USNM 554361
Description Frond fragment once pinnate. Pinnules opposite, inclined, excurrent. Pinnule shape ovate, length 8mm, width 4mm; apex rounded, symmetrical; base obtuse, auriculate, anadromous. Margin smooth. Venation open, pinnate, secondary veins subopposite, excurrent, ascending, twice forked, terminating at margin.

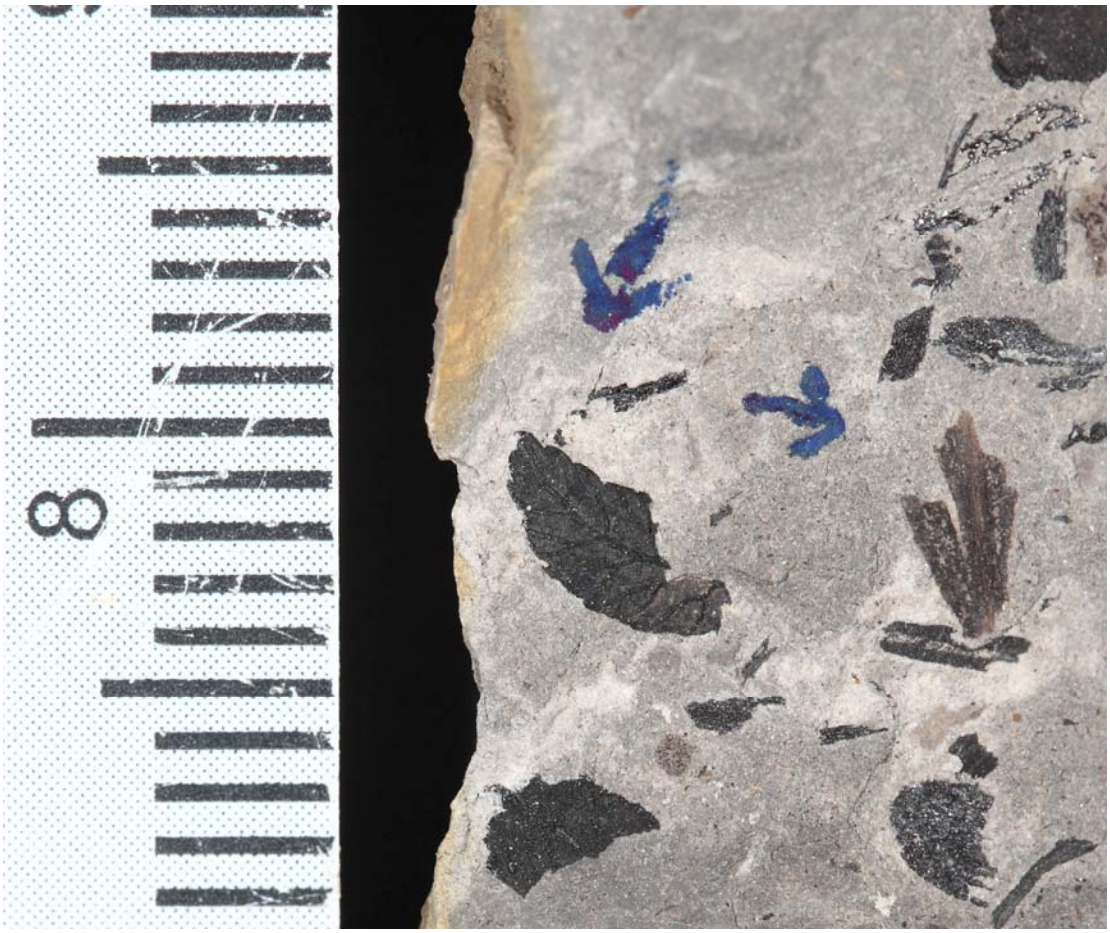
Morphotype CVF17 USNM 554487
Pinnules minute, pinnatisect, about as long as wide, venation open.

Morphotype CVF18 USNM 554521
Description: Frond fragment pinnate. Pinnules inclined, excurrent. Pinnule shape ovate, slightly curved toward apex, length 4.5mm, width 2mm; apex rounded, symmetrical; base obtuse, slightly auriculate, anadromous. Margin smooth. Venation open, pinnate, secondary veins subopposite, excurrent, ascending, forked, terminating at margin.



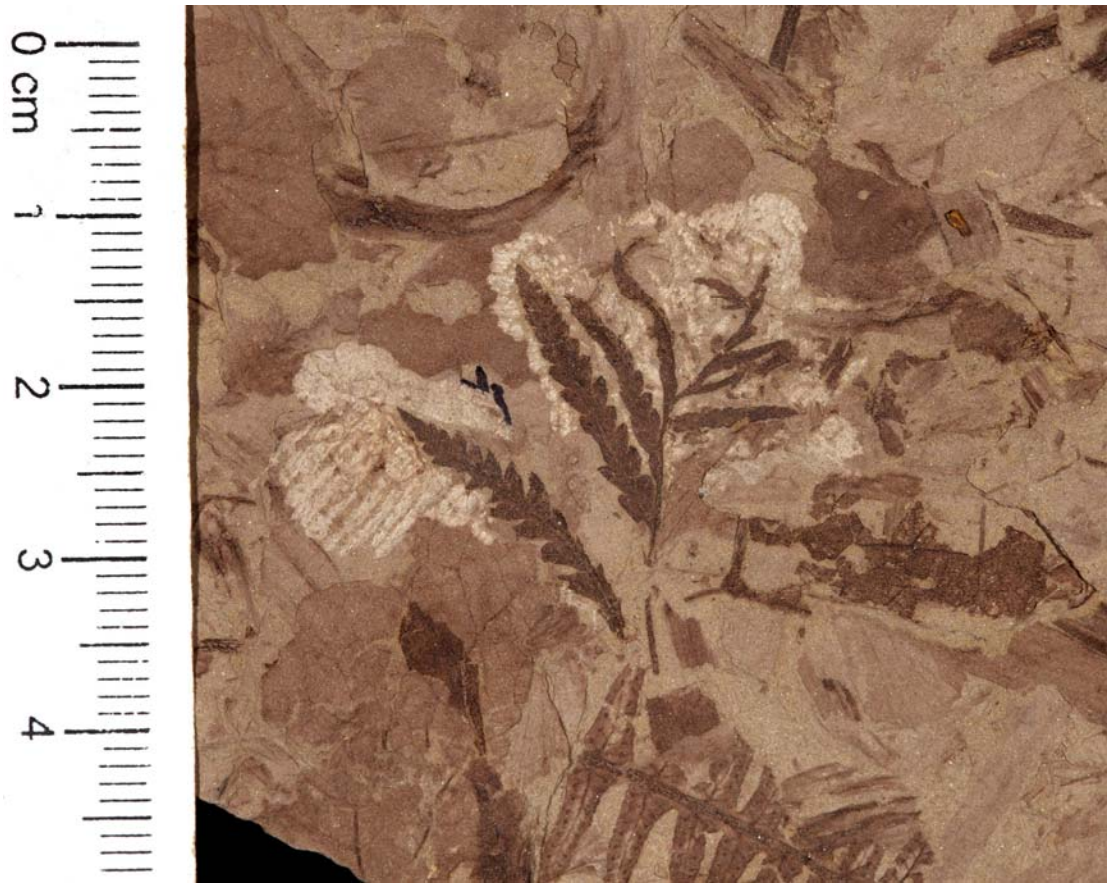
Morphotype CVF19 USNM 554520
Description: Fragment of lamina. Venation reticulate. Primary veins dichotomous, Tertiary veins percurrent, quaternary veins forming a dense reticulum with square areoles.
Affinity: *Dipteris*

Morphotype CVF20 USNM 554538
Description: Pinnule shape ovate, curved toward apex; apex acute, sharp; base unknown. Margin toothed. Venation open, pinnate, secondary veins subopposite, excurrent, ascending, once forked, terminating at margin.

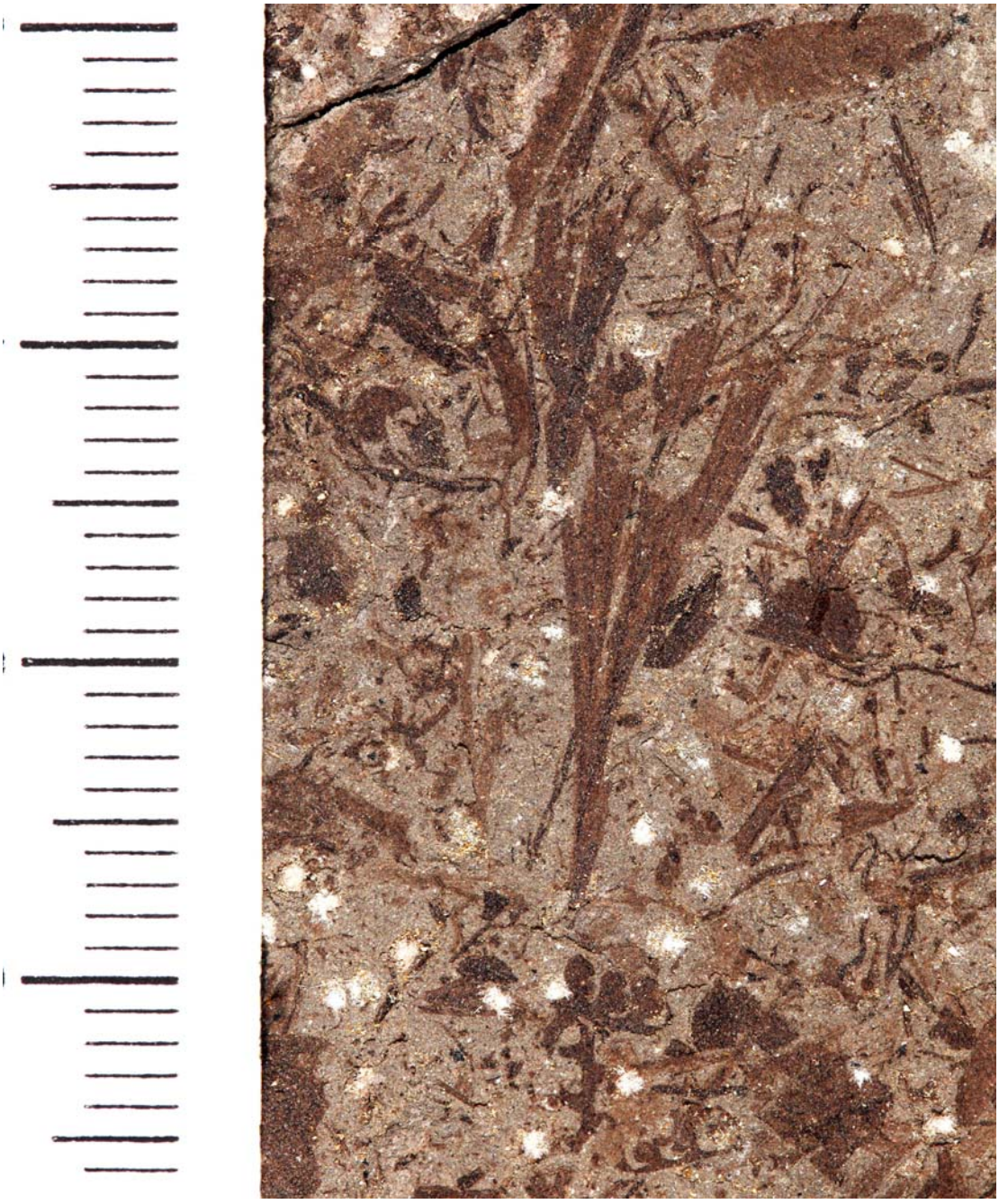


Morphotype CVF21 USNM 554005
Description: Frond fragment pinnate. Pinnules alternate, adpressed, decurrent. Pinnule shape ovate-lanciolate, length 6mm, width 1.5mm; apex acute, symmetrical; base acute. Margin toothed. Venation open, dichotomizing, midvein indistinct, veins terminating at margin.

Morphotype CVF22 USNM 554090
Description: Frond fragment pinnate pinnatifid. Pinnae excurrent, ascending, alternate. Pinna shape lanciolate, length 16mm, width 2.5mm; apex acute, straight, symmetrical; base acute, basiscopic margin decurrent to rachis. Pinnules subopposite, inclined, triangular; Pinnule apex acute, straight; sinuses acute, sharp.



Morphotype CVF23 USNM 554028
Description: lamina narrow, deeply dissected, dichotomous; segments 1-2mm wide. Venation open dichotomous, angle of dichotomies 5-10°, veins terminate at margin. Margin irregularly toothed. Teeth simple, supplied by single vein.



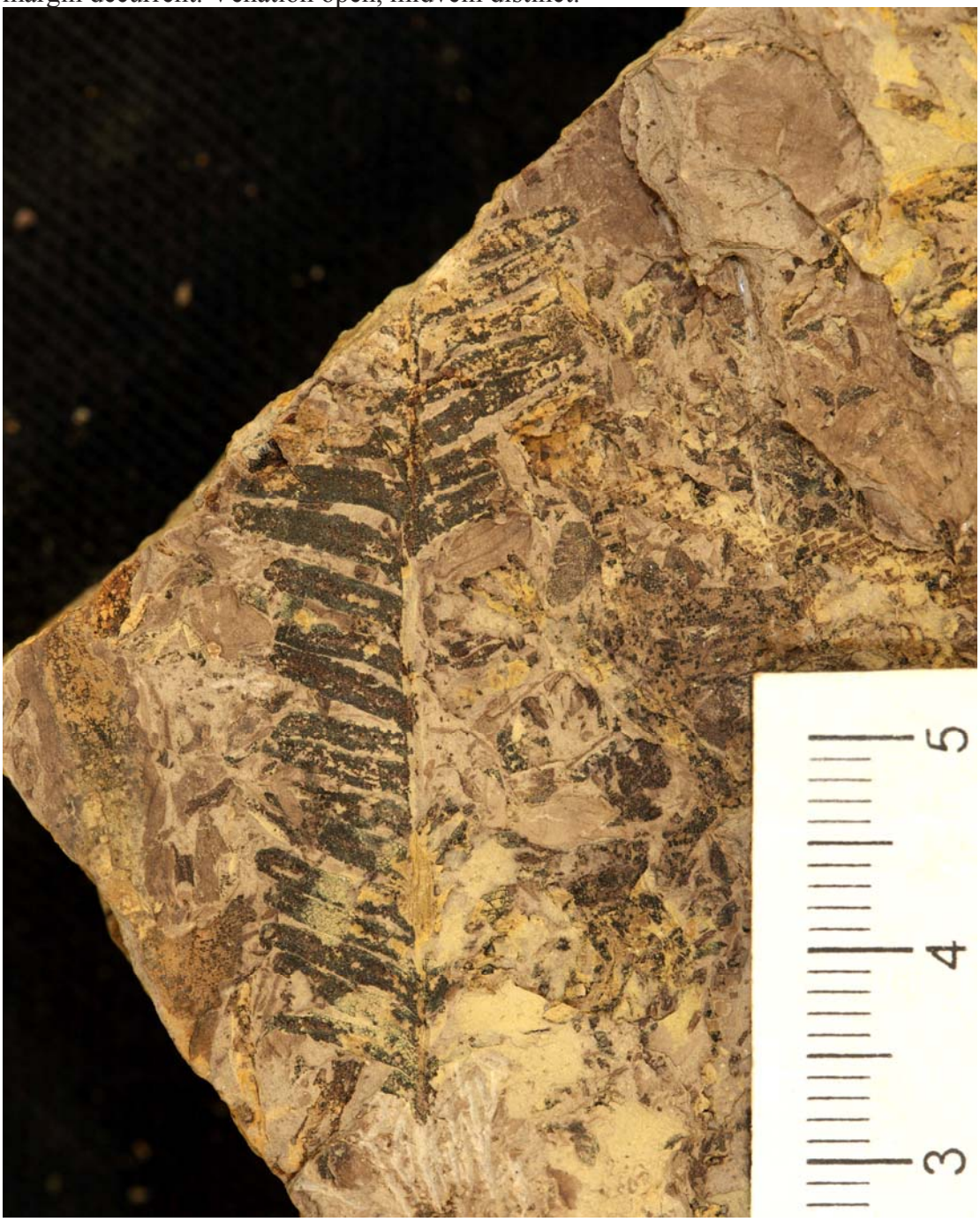
Morphotype CVF24 USNM 554034
Description: Frond fragment pinnatifid. Pinna length unknown, width 1cm. Pinnule shape triangular, angle inclined, apex and sinus rounded. Venation open, pinnate, secondary veins alternate, inclined, once forked, terminating at margin.

Morphotype CVF25 USNM
Description: Frond fragment pinnate, Pinnules alternate, perpendicular, excurrent. Pinnule shape lanciolate, slightly curved, length up to 10mm, width 3mm; apex obtuse, rounded, base slightly contracted, broadly attached, symmetrical. Margin serrate. Venation open; primary venation pinnate; secondary veins simple, alternate, inclined, straight, terminating at margin.

Morphotype CVF26
Description: Pinnate. Pinnules alternate, perpendicular, excurrent, curved toward apex. Pinnules ovate, length 6mm, width 2mm; apex acute, base obtuse. Margin toothed, teeth broad. Venation open, pinnate

Morphotype CVF27 USNM 554132
Description: Frond fragment pinnate, alternate, adpressed. Pinnule shape ovate lanciolate, length 10mm width 1mm, apex acute base acute, broadly attached, decurrent. Margin smooth.

Morphotype CVF28 USNM 554162
Description: Frond fragment pinnatisect. Pinnules densely spaced, 5 pinnules per cm, Pinnule arrangement subopposite, excurrent, inclined. Pinnule shape elongate, length 8mm, width 1.5mm, apex rounded to truncate, base broadly attached, basiscopic margin decurrent. Venation open, midvein distinct.



Morphotype CVF31 USNM 554420
Description: Pinna pinnatisect. Pinnules subopposite, inclined, decurrent. Pinnule shape triangular, curved toward apex, length 8mm, width at base 3.5mm; apex rounded; base broadly attached. Margin smooth. Venation pinnate.

Morphotype CVF32 USNM TBD, block ID: NAJ 1203I
Description: Pinna pinnate. Pinnules subopposite, perpendicular, excurrent. Pinnule shape oblong, length 5mm, width 2.5mm; apex rounded, base auriculate, basiscopic margin decurrent to rachis; terminal pinnule wider than long, apex rounded, base auriculate. Margin smooth. Venation open, pinnate, secondary veins dichotomous, terminating at margin.

Morphotype CVF33 USNM 554704
Description: Fronds at least twice pinnate pinnatifid. Primary pinnae alternate, anadromous, adpressed, decurrent. Secondary pinnae alternate, adpressed, decurrent. Pinnules alternate, adpressed, decurrent. Pinnules narrow, length 1-2mm, width <1mm; apex sharp, sinuses sharp, venation open.
Affinity: *Onychiopsis*

Morphotype CVF36 USNM 554711
Description: Pinnae pinnatisect. Pinnules subopposite, perpendicular, excurrent. Pinnule shape lanciolate, length 14mm, width 1mm; apex rounded; base broadly attached. Margin untoothed. Venation open.

Morphotype CVF37 USNM 554717
Description: Pinna pinnate. Pinnules inclined. Pinnule shape ovate-lanciolate, length >16mm, width 4mm; apex acute. Margin toothed. Venation pinnate, secondary veins alternate, decurrent, ascending, dichotomous. Veins terminating at margin or sori. Sori abaxial, elliptic, one per tooth.

Morphotype CVF40 USNM 554524
Description: Pinnae once pinnate. Pinnules subopposite to alternate, ascending, decurrent. Pinnule shape ovate, length up to 4mm, width up to 3mm; apex acute, straight, symmetrical; base acute, basiscopic margin decurrent. Margin lobed. Venation catadromous.

Morphotype CVF42 USNM 554623
Description: Pinnae pinnatisect. Pinnules subopposite, ascending, excurrent. Pinnule shape lanciolate, length 18mm, width 1mm; apex rounded; base broadly attached. Margin untoothed. Venation open, midvein distinct.

Morphotype CVF47 USNM 554627
Description: Pinnule obovate, length 6mm, width 3.5mm; apex obtuse; base acute. Margin toothed. Venation pinnate, secondary veins alternate, ascending, excurrent, slightly curved toward apex, terminating at apex of tooth.

Morphotype CVE1 USNM 554629
Description: herbaceous shoot with longitudinal striations; width 6mm; narrow, elongate, triangular leaves forming a collar; leaves subtended by herbaceous branches 2mm wide.
Interpretation: *Equisetum*

Appendix II

Morphotype occurrence data in long format. Each row constitutes an occurrence of a morphotype on a block of rock. Scores in the count, cover, and quadrat columns were used to compare the three different abundance metrics.

Plant fossil occurrence data in long format								
Unit	Enviro-nment.	USNM locality	collection event	USNM block	ID	count	cover	quadrat
Sykes Mtn	fill	43903	1001	553831	CVF2	1	5	1
Sykes Mtn	fill	43903	1001	553832	CVCo1	1	5	1
Sykes Mtn	fill	43903	1002	553833	CVCo1	8	5	1
Sykes Mtn	fill	43903	1002	553833	CVCo1	1	5	1
Sykes Mtn	fill	43903	1002	553834	CVCo1	2	5	1
Sykes Mtn	splay	43904	1004	553836	CVA6	3	5	1
Sykes Mtn	splay	43904	1004	553836	CVA7	1	1	1
Sykes Mtn	splay	43904	1004	553836	CVF5	1	1	1
Sykes Mtn	splay	43904	1004	553837	CVA6	5	5	1
Sykes Mtn	splay	43904	1004	553838	CVA6	2	5	1
Sykes Mtn	splay	43904	1004	553839	CVA6	2	5	1
Sykes Mtn	splay	43904	1004	553839	CVF6	1	1	1
Sykes Mtn	splay	43904	1004	553840	CVA6	1	5	1
Sykes Mtn	splay	43904	1004	553841	CVA8	1	4	1
Sykes Mtn	splay	43904	1004	553841	CVA6	2	3	1
Sykes Mtn	splay	43904	1004	553841	CVF5	1	1	1
Sykes Mtn	splay	43904	1004	553843	CVA6	3	5	1
Sykes Mtn	splay	43904	1004	553843	CVF6	1	1	1
Sykes Mtn	splay	43904	1004	553844	CVA6	2	5	1
Sykes Mtn	splay	43904	1004	553845	CVA6	1	5	1
Sykes Mtn	splay	43904	1004	553846	CVCo1	1	5	1
Sykes Mtn	splay	43904	1004	553847	CVCo1	3	5	1
Sykes Mtn	splay	43904	1004	553848	CVF5	1	5	1
Sykes Mtn	splay	43904	1004	553849	CVA6	1	5	1
Sykes Mtn	splay	43904	1004	553850	CVF5	1	5	1
Sykes Mtn	splay	43904	1004	553851	CVA6	2	5	1
Sykes Mtn	splay	43904	1004	553852	CVA6	3	5	1
Sykes Mtn	splay	43904	1004	553853	CVA6	5	5	1
Sykes Mtn	fill	43906	1006	553854	CVF5	3	4	1
Sykes Mtn	fill	43906	1006	553854	CVA9	4	3	1
Sykes Mtn	fill	43906	1006	553855	CVA9	1	5	1
Sykes Mtn	fill	43906	1006	553856	CVF3	1	5	1

Sykes Mtn	fill	43906	1006	553857	CVF5	3	4	1
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Sykes Mtn	fill	43906	1006	553857	CVA9	1	1	1
Sykes Mtn	fill	43906	1006	553858	CVF5	2	5	1
Sykes Mtn	fill	43906	1006	553858	CVF4	4	2	1
Sykes Mtn	fill	43906	1006	553859	CVF3	1	3	1
Sykes Mtn	fill	43906	1006	553859	CVA10	1	4	1
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Sykes Mtn	fill	43906	1006	553860	CVF5	6	5	1
Sykes Mtn	fill	43906	1006	553861	CVF5	1	5	1
Sykes Mtn	fill	43906	1006	553926	CVF4	7	5	1
Sykes Mtn	fill	43906	1006	553927	CVF4	1	5	1
Sykes Mtn	fill	43905	1005	553862	CVCo1	4	1	1
Sykes Mtn	fill	43905	1005	553863	CVF4	2	3	1
Sykes Mtn	fill	43905	1005	553863	CVA3	1	4	1
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Sykes Mtn	fill	43907	1007	553866	CVA3	2	1	1
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lower Cloverly	lake	43908	1008	553909	CVCy1	23	5	1
lower Cloverly	lake	43908	1008	553910	CVCy1	12	5	1
lower Cloverly	lake	43908	1008	553911	CVCy1	12	5	1
lower Cloverly	lake	43908	1008	553912	CVCy1	1	5	1
lower Cloverly	lake	43908	1008	553913	CVCy1	26	5	1
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Sykes Mtn	splay	43904	1012	553958	CVA6	1	5	1
Sykes Mtn	splay	43904	1012	553958	CVCo1	1	1	1
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Sykes Mtn	splay	43904	1012	553959	CVA6	3	5	1
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Sykes Mtn	splay	43904	1012	553961	CVA6	2	5	1
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Sykes Mtn	splay	43904	1012	553967	CVA6	1	5	1
Sykes Mtn	splay	43904	1012	553967	CVCo1	1	1	1
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Sykes Mtn	splay	43904	1012	553971	CVF6	1	5	1
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Sykes Mtn	splay	43904	1012	553979	CVCo1	2	1	1
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Sykes Mtn	splay	43904	1012	558987	CVA6	1	5	1
lower Cloverly	lake	43912	SLWPP1004	553988	CVF1	3	4	1
lower Cloverly	lake	43912	SLWPP1004	553988	CVF19	2	3	1
lower Cloverly	lake	43912	SLWPP1004	553989	CVF1	7	3	1
lower Cloverly	lake	43912	SLWPP1004	553989	CVCy1	8	4	1
lower Cloverly	lake	43912	SLWPP1004	553989	CVF19	1	1	1
lower Cloverly	lake	43912	SLWPP1004	553990	CVF1	10	5	1
lower Cloverly	lake	43912	SLWPP1004	553991	CVF1	1	5	1
lower Cloverly	lake	43912	SLWPP1004	553992	CVF1	2	5	1
lower Cloverly	lake	43912	SLWPP1004	553995	CVCy1	23	5	1
lower Cloverly	fill	43911	1013	553996	CVF1	1	5	1
lower Cloverly	fill	43911	1013	553997	CVF1	4	5	1
lower Cloverly	fill	43911	1013	553998	CVF1	7	5	1
lower Cloverly	fill	43911	1013	553999	CVF1	7	5	1
lower Cloverly	fill	43911	1013	554000	CVF1	1	5	1
lower Cloverly	fill	43911	1013	554001	CVF1	1	5	1
lower Cloverly	fill	43911	1013	554002	CVF1	1	5	1
Sykes Mtn	fill	43913	1101	554003	CVA16	1	5	1
Sykes Mtn	fill	43913	1101	554004	CVF3	1	1	1
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Sykes Mtn	fill	43915	1103	554144	CVF2	1	5	1
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Sykes Mtn	fill	43915	1103	554146	CVCo1	1	5	1
Sykes Mtn	fill	43915	1103	554148	CVCo1	3	5	1
Sykes Mtn	fill	43915	1103	554149	CVCo1	8	1	1
Sykes Mtn	fill	43915	1103	554149	CVA11	1	5	1
Sykes Mtn	fill	43915	1103	554149	CVA20	1	1	1
Sykes Mtn	fill	43915	1103	554150	CVA21	1	5	1
Sykes Mtn	fill	43915	1103	554151	CVCo1	8	5	1
Sykes Mtn	fill	43915	1103	554153	CVA3	1	4	1

Sykes Mtn	fill	43915	1103	554153	CVCo1	1	3	1
Sykes Mtn	fill	43915	1103	554154	CVA5	1	4	1
Sykes Mtn	fill	43915	1103	554154	CVCo1	4	3	1
Sykes Mtn	fill	43915	1103	554155	CVA20	2	5	1
Sykes Mtn	fill	43915	1103	554155	CVF26	1	1	1
Sykes Mtn	fill	43915	1103	554156	CVA22	1	5	1
Sykes Mtn	fill	43915	1103	554156	CVCo1	5	1	1
Sykes Mtn	fill	43915	1103	554156	CVA3	1	1	1
Sykes Mtn	fill	43915	1103	554157	CVF4	1	3	1
Sykes Mtn	fill	43915	1103	554157	CVA3	3	4	1
Sykes Mtn	fill	43915	1103	554158	CVF26	1	2	1
Sykes Mtn	fill	43915	1103	554158	CVA3	1	3	1
Sykes Mtn	fill	43915	1103	554158	CVCo1	2	2	1
Sykes Mtn	fill	43915	1103	554159	CVCo1	4	5	1
Sykes Mtn	fill	43915	1103	554160	CVCo1	4	5	1
Sykes Mtn	fill	43915	1103	554162	CVCo1	20	4	1
Sykes Mtn	fill	43915	1103	554162	CVF28	1	3	1
Sykes Mtn	fill	43915	1103	554163	CVA11	1	5	1
Sykes Mtn	fill	43915	1103	554164	CVF26	1	5	1
Sykes Mtn	fill	43915	1103	554165	CVA3	4	4	1
Sykes Mtn	fill	43915	1103	554165	CVCo1	6	3	1
Sykes Mtn	fill	43915	1103	554166	CVCo1	10	5	1
Sykes Mtn	fill	43915	1103	554166	CVA3	2	1	1
Sykes Mtn	fill	43915	1103	554166	CVA20	1	1	1
Sykes Mtn	splay	43916	1104	554167	CVA6	2	5	1
Sykes Mtn	splay	43916	1104	554168	CVA6	2	5	1
Sykes Mtn	splay	43916	1104	554169	CVA6	1	4	1
Sykes Mtn	splay	43916	1104	554169	CVF6	1	3	1
Sykes Mtn	splay	43916	1104	554170	CVF28	1	5	1
Sykes Mtn	splay	43916	1104	554171	CVF12	1	5	1
Sykes Mtn	splay	43917	1105	554176	CVA6	5	5	1
Sykes Mtn	splay	43917	1105	554177	CVA6	6	5	1
Sykes Mtn	splay	43917	1105	554178	CVA6	4	5	1
Sykes Mtn	splay	43917	1105	554179	CVA6	4	5	1
Sykes Mtn	splay	43917	1105	554180	CVA6	1	5	1
Sykes Mtn	splay	43917	1105	554180	CVCo1	1	1	1
Sykes Mtn	splay	43917	1105	554181	CVA6	4	5	1
Sykes Mtn	splay	43917	1105	554181	CVF12	1	1	1
Sykes Mtn	splay	43917	1105	554181	CVCo1	1	1	1
Sykes Mtn	splay	43917	1105	554182	CVA6	3	5	1
Sykes Mtn	splay	43917	1105	554183	CVA6	6	5	1

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Sykes Mtn	splay	43917	1105	554185	CVA6	1	5	1
Sykes Mtn	splay	43917	1105	554186	CVF21	1	5	1
Sykes Mtn	splay	43917	1105	554189	CVA6	1	5	1
Sykes Mtn	splay	43917	1105	554190	CVA6	1	5	1
Sykes Mtn	splay	43917	1105	554191	CVA6	2	5	1
Sykes Mtn	splay	43917	1105	554192	CVA6	4	5	1
Sykes Mtn	splay	43917	1105	554193	CVA6	1	5	1
Sykes Mtn	splay	43917	1105	554194	CVA6	4	5	1
Sykes Mtn	splay	43917	1105	554195	CVA6	4	5	1
Sykes Mtn	splay	43917	1105	554196	CVA6	4	5	1
Sykes Mtn	splay	43917	1105	554197	CVA6	1	5	1
Sykes Mtn	splay	43917	1105	554199	CVF6	1	5	1
Sykes Mtn	splay	43917	1105	554202	CVA6	2	5	1
Sykes Mtn	splay	43917	1105	554203	CVA6	2	5	1
Sykes Mtn	splay	43917	1105	554204	CVF6	1	1	1
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Sykes Mtn	splay	43917	1105	554205	CVA6	1	5	1
Sykes Mtn	splay	43917	1105	554206	CVF12	2	5	1
Sykes Mtn	splay	43917	1105	554207	CVF25	1	5	1
Sykes Mtn	splay	43917	1105	554208	CVF12	1	5	1
Sykes Mtn	splay	43917	1105	554209	CVA6	1	5	1
Sykes Mtn	splay	43917	1105	554210	CVA6	1	5	1
Sykes Mtn	splay	43917	1105	554211	CVF29	1	5	1
Sykes Mtn	splay	43917	1105	554213	CVA6	1	5	1
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Sykes Mtn	splay	43917	1105	554216	CVA6	3	5	1
Sykes Mtn	splay	43917	1105	554217	CVA6	1	5	1
Sykes Mtn	splay	43917	1105	554218	CVA6	2	5	1
Sykes Mtn	splay	43917	1105	554219	CVA6	1	5	1
Sykes Mtn	splay	43917	1105	554221	CVA6	1	5	1
Sykes Mtn	splay	43917	1105	554222	CVA6	1	5	1
Sykes Mtn	splay	43917	1105	554223	CVA6	1	5	1
Sykes Mtn	splay	43917	1105	554224	CVA6	1	5	1
Sykes Mtn	splay	43917	1105	554225	CVA6	1	5	1
Sykes Mtn	splay	43917	1105	554226	CVA6	1	5	1
Sykes Mtn	splay	43917	1105	554227	CVA6	2	5	1
Sykes Mtn	splay	43917	1105	554228	CVA6	1	5	1
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Sykes Mtn	splay	43917	1105	554230	CVA6	1	5	1

Sykes Mtn	splay	43917	1105	554231	CVA6	1	5	1
Sykes Mtn	splay	43917	1105	554232	CVA6	2	5	1
Sykes Mtn	splay	43917	1105	554233	CVA6	1	5	1
Sykes Mtn	splay	43917	1105	554234	CVA6	2	5	1
Sykes Mtn	splay	43917	1105	554236	CVA6	5	5	1
Sykes Mtn	splay	43917	1105	554236	CVA7	1	2	1
Sykes Mtn	splay	43917	1105	554237	CVA6	1	5	1
Sykes Mtn	splay	43917	1105	554238	CVA6	2	5	1
Sykes Mtn	splay	43917	1105	554239	CVA6	5	5	1
Sykes Mtn	splay	43917	1105	554240	CVA6	1	5	1
Sykes Mtn	splay	43917	1105	554241	CVA6	1	5	1
Sykes Mtn	splay	43917	1105	554242	CVF6	1	5	1
Sykes Mtn	splay	43917	1105	554243	CVF12	2	5	1
Sykes Mtn	splay	43917	1105	554245	CVA6	1	5	1
Sykes Mtn	splay	43917	1105	554246	CVA6	1	5	1
Sykes Mtn	splay	43917	1105	554250	CVA6	4	5	1
Sykes Mtn	splay	43917	1105	554251	CVA6	1	5	1
Sykes Mtn	splay	43917	1105	554252	CVF6	1	5	1
Sykes Mtn	splay	43917	1105	554254	CVA6	2	5	1
Sykes Mtn	splay	43917	1105	554255	CVF25	1	5	1
Sykes Mtn	splay	43917	1105	554257	CVA6	1	5	1
Sykes Mtn	splay	43917	1105	554258	CVA6	3	5	1
Sykes Mtn	splay	43917	1105	554258	CVF25	1	1	1
Sykes Mtn	splay	43917	1105	554259	CVF6	1	5	1
Sykes Mtn	splay	43917	1105	554260	CVA6	7	5	1
Sykes Mtn	splay	43917	1105	554261	CVF25	1	5	1
Sykes Mtn	splay	43917	1105	554262	CVA6	1	5	1
Sykes Mtn	splay	43917	1105	554263	CVA6	1	5	1
Sykes Mtn	splay	43917	1105	554264	CVA6	3	5	1
Sykes Mtn	splay	43917	1105	554265	CVA6	2	5	1
Sykes Mtn	splay	43917	1105	554266	CVA6	1	5	1
Sykes Mtn	splay	43917	1105	554267	CVA6	3	5	1
Sykes Mtn	splay	43917	1105	554269	CVA6	2	5	1
Sykes Mtn	splay	43917	1105	554270	CVA6	1	5	1
Sykes Mtn	fill	43918	1106	554273	CVA23	1	5	1
Sykes Mtn	fill	43918	1106	554274	CVCo1	1	5	1
Sykes Mtn	fill	43918	1106	554276	CVCo1	2	1	1
Sykes Mtn	fill	43918	1106	554276	CVA23	2	5	1
Sykes Mtn	fill	43918	1106	554277	CVA6	1	5	1
Sykes Mtn	fill	43919	1107	554278	CVF4	1	5	1
Sykes Mtn	fill	43919	1107	554279	CVCo1	10	5	1

Sykes Mtn	fill	43919	1107	554280	CVCo1	2	4	1
Sykes Mtn	fill	43919	1107	554280	CVF4	1	3	1
Sykes Mtn	fill	43919	1107	554281	CVCo1	2	1	1
Sykes Mtn	fill	43919	1107	554282	CVCo1	2	5	1
Sykes Mtn	fill	43919	1107	554283	CVCo1	5	5	1
Sykes Mtn	fill	43919	1107	554284	CVCo1	8	5	1
Sykes Mtn	fill	43919	1107	554285	CVCo1	5	5	1
Sykes Mtn	fill	43919	1107	554285	CVF4	1	1	1
Sykes Mtn	fill	43919	1107	554286	CVCo1	5	5	1
Sykes Mtn	fill	43919	1107	554287	CVCo1	4	5	1
Sykes Mtn	fill	43919	1107	554288	CVCo1	6	3	1
Sykes Mtn	fill	43919	1107	554288	CVF4	7	4	1
Sykes Mtn	fill	43919	1107	554289	CVCo1	3	5	1
Sykes Mtn	fill	43919	1107	554290	CVCo1	5	5	1
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Sykes Mtn	fill	43919	1107	554293	CVF4	2	5	1
Sykes Mtn	fill	43919	1107	554294	CVCo1	2	4	1
Sykes Mtn	fill	43919	1107	554294	CVF4	1	3	1
Sykes Mtn	fill	43919	1107	554295	CVF4	2	4	1
Sykes Mtn	fill	43919	1107	554295	CVCo1	3	3	1
Sykes Mtn	fill	43919	1107	554296	CVCo1	3	1	1
Sykes Mtn	fill	43919	1107	554297	CVCo1	3	5	1
Sykes Mtn	fill	43919	1107	554297	CVF4	1	2	1
Sykes Mtn	fill	43919	1107	554298	CVF4	1	5	1
Sykes Mtn	fill	43919	1107	554299	CVF4	1	5	1
Sykes Mtn	fill	43919	1107	554300	CVCo1	2	5	1
Sykes Mtn	fill	43919	1107	554301	CVCo1	3	4	1
Sykes Mtn	fill	43919	1107	554301	CVF4	2	3	1
Sykes Mtn	fill	43919	1107	554302	CVCo1	3	5	1
Sykes Mtn	fill	43919	1107	554303	CVCo1	3	5	1
Sykes Mtn	fill	43919	1107	554304	CVCo1	9	5	1
Sykes Mtn	fill	43919	1107	554305	CVCo1	3	5	1
Sykes Mtn	fill	43919	1107	554306	CVCo1	7	5	1
Sykes Mtn	fill	43919	1107	554307	CVCo1	10	2	1
Sykes Mtn	fill	43919	1107	554308	CVCo1	3	5	1
Sykes Mtn	fill	43919	1107	554309	CVCo1	4	4	1
Sykes Mtn	fill	43919	1107	554309	CVF4	4	3	1
Sykes Mtn	fill	43919	1107	554310	CVCo1	1	5	1
Sykes Mtn	fill	43919	1107	554311	CVF4	1	5	1

Sykes Mtn	fill	43919	1107	554312	CVCo1	5	5	1
Sykes Mtn	fill	43919	1107	554313	CVCo1	2	5	1
Sykes Mtn	fill	43919	1107	554314	CVCo1	1	5	1
Sykes Mtn	fill	43919	1107	554315	CVCo1	3	5	1
Sykes Mtn	fill	43919	1107	554316	CVCo1	20	5	1
Sykes Mtn	fill	43919	1107	554317	CVF4	2	5	1
Sykes Mtn	fill	43919	1107	554318	CVCo1	2	5	1
Sykes Mtn	fill	43919	1107	554319	CVCo1	5	5	1
Sykes Mtn	fill	43919	1107	554320	CVCo1	1	5	1
Sykes Mtn	fill	43919	1107	554321	CVCo1	3	2	1
Sykes Mtn	fill	43919	1107	554321	CVA24	2	5	1
Sykes Mtn	fill	43919	1107	554322	CVA24	1	5	1
Sykes Mtn	fill	43919	1107	554323	CVCo1	4	5	1
Sykes Mtn	fill	43919	1107	554324	CVCo1	3	4	1
Sykes Mtn	fill	43919	1107	554324	CVF4	2	3	1
Sykes Mtn	fill	43919	1107	554325	CVF4	1	5	1
Sykes Mtn	fill	43919	1107	554326	CVF4	2	5	1
lower Cloverly	lake	43920	1108	554339	CVCy1	7	5	1
lower Cloverly	lake	43920	1108	554339	CVF1	1	1	1
lower Cloverly	lake	43920	1108	554339	CVF19	1	1	1
lower Cloverly	lake	43920	1108	554340	CVCy1	6	5	1
lower Cloverly	lake	43920	1108	554341	CVCy1	7	5	1
lower Cloverly	lake	43920	1108	554341	CVCo2	1	1	1
lower Cloverly	lake	43920	1108	554341	CVF1	2	1	1
lower Cloverly	lake	43920	1108	554342	CVF1	1	5	1
lower Cloverly	lake	43920	1108	554343	CVF14	2	4	1
lower Cloverly	lake	43920	1108	554343	CVF1	1	1	1
lower Cloverly	lake	43920	1108	554344	CVI1	2	5	1
lower Cloverly	lake	43920	1108	554345	CVCy1	4	5	1
lower Cloverly	lake	43920	1108	554345	CVI1	2	1	1
lower Cloverly	lake	43920	1108	554346	CVCy1	1	5	1
lower Cloverly	lake	43920	1108	554347	CVF1	1	5	1
lower Cloverly	lake	43920	1108	554348	CVI1	11	5	1
lower Cloverly	lake	43920	1108	554348	CVCo6	1	2	1
lower Cloverly	lake	43920	1108	554348	CVCo4	1	1	1
lower Cloverly	lake	43920	1108	554348	CVCy1	1	1	1
lower Cloverly	lake	43920	1108	554349	CVF1	1	1	1
lower Cloverly	lake	43920	1108	554349	CVI1	11	5	1
lower Cloverly	lake	43920	1108	554349	CVCo6	2	2	1
lower Cloverly	lake	43920	1108	554349	CVF18	1	1	1
lower Cloverly	lake	43920	1108	554350	CVF1	1	5	1

lower Cloverly	lake	43920	1108	554351	CVF1	1	5	1
lower Cloverly	lake	43920	1108	554352	CVF19	1	4	1
lower Cloverly	lake	43920	1108	554352	CVCo6	1	3	1
lower Cloverly	lake	43920	1108	554353	CVF1	1	1	1
lower Cloverly	lake	43920	1108	554353	CVCy1	4	5	1
lower Cloverly	lake	43920	1108	554354	CVF1	2	5	1
lower Cloverly	lake	43920	1108	554355	CVI1	1	2	1
lower Cloverly	lake	43920	1108	554355	CVCo2	1	2	1
lower Cloverly	lake	43920	1108	554356	CVCo6	2	1	1
lower Cloverly	lake	43920	1108	554356	CVCy2	2	4	1
lower Cloverly	lake	43920	1108	554356	CVI1	7	3	1
lower Cloverly	lake	43920	1108	554356	CVCo4	1	1	1
lower Cloverly	lake	43920	1108	554356	CVCo2	2	2	1
lower Cloverly	lake	43920	1108	554356	CVF1	1	1	1
lower Cloverly	lake	43920	1108	554357	CVCo2	1	4	1
lower Cloverly	lake	43920	1108	554357	CVI1	2	3	1
lower Cloverly	lake	43920	1108	554358	CVF19	1	4	1
lower Cloverly	lake	43920	1108	554358	CVF17	1	1	1
lower Cloverly	lake	43920	1108	554358	CVF1	1	2	1
lower Cloverly	lake	43920	1108	554359	CVCo3	1	5	1
lower Cloverly	lake	43920	1108	554360	CVF1	2	4	1
lower Cloverly	lake	43920	1108	554360	CVI1	4	3	1
lower Cloverly	lake	43920	1108	554360	CVF18	1	1	1
lower Cloverly	lake	43920	1108	554361	CVF16	1	4	1
lower Cloverly	lake	43920	1108	554361	CVI1	2	1	1
lower Cloverly	lake	43920	1108	554362	CVCo6	1	5	1
lower Cloverly	lake	43920	1108	554362	CVI1	1	2	1
lower Cloverly	lake	43920	1108	554363	CVI1	3	4	1
lower Cloverly	lake	43920	1108	554363	CVF19	1	3	1
lower Cloverly	lake	43921	1109	554464	CVF18	1	5	1
lower Cloverly	lake	43921	1109	554465	CVF1	5	3	1
lower Cloverly	lake	43921	1109	554465	CVCy1	6	4	1
lower Cloverly	lake	43921	1109	554466	CVCy1	8	5	1
lower Cloverly	lake	43921	1109	554467	CVCy1	4	5	1
lower Cloverly	lake	43921	1109	554467	CVCo2	1	2	1
lower Cloverly	lake	43921	1109	554468	CVF18	1	1	1
lower Cloverly	lake	43921	1109	554468	CVCy1	3	5	1
lower Cloverly	lake	43921	1109	554469	CVF13	1	5	1
lower Cloverly	lake	43921	1109	554470	CVCy1	10	5	1
lower Cloverly	lake	43921	1109	554471	CVF19	1	5	1
lower Cloverly	lake	43921	1109-1	554473	CVCy1	1	5	1

lower Cloverly	lake	43921	1109-1	554474	CVCy1	14	5	1
lower Cloverly	lake	43921	1109-1	554474	CVF1	2	1	1
lower Cloverly	lake	43921	1109-1	554475	CVF1	3	5	1
lower Cloverly	lake	43921	1109-1	554475	CVCo2	1	1	1
lower Cloverly	lake	43921	1109-1	554476	CVCy1	18	5	1
lower Cloverly	lake	43921	1109-1	554477	CVCo2	2	4	1
lower Cloverly	lake	43921	1109-1	554477	CVF1	3	2	1
lower Cloverly	lake	43921	1109-1	554477	CVI1	4	2	1
lower Cloverly	lake	43921	1109-1	554478	CVCo2	1	5	1
lower Cloverly	lake	43921	1109-1	554478	CVF1	5	2	1
lower Cloverly	lake	43921	1109-1	554479	CVCy1	15	5	1
lower Cloverly	lake	43921	1109-1	554480	CVCo2	2	5	1
lower Cloverly	lake	43921	1109-1	554480	CVF1	1	1	1
lower Cloverly	lake	43921	1109-1	554481	CVCy1	14	5	1
lower Cloverly	lake	43921	1109-1	554482	CVCo2	3	5	1
lower Cloverly	lake	43921	1109-1	554482	CVF1	2	1	1
lower Cloverly	lake	43921	1109-1	554483	CVF1	10	5	1
lower Cloverly	lake	43921	1109-1	554484	CVF1	15	5	1
lower Cloverly	lake	43921	1109-1	554485	CVCo2	1	5	1
lower Cloverly	lake	43921	1109-1	554485	CVF1	1	1	1
lower Cloverly	lake	43921	1109-1	554486	CVCy1	2	5	1
lower Cloverly	lake	43921	1109-1	554487	CVF17	1	5	1
lower Cloverly	lake	43921	1109-2	554488	CVCy1	26	5	1
lower Cloverly	lake	43921	1109-2	554488	CVF1	1	1	1
lower Cloverly	lake	43921	1109-2	554489	CVCy1	400	5	1
lower Cloverly	lake	43921	1109-2	554490	CVCy1	3	5	1
lower Cloverly	lake	43921	1109-2	554490	CVF1	1	2	1
lower Cloverly	lake	43921	1109-2	554491	CVCy1	68	5	1
lower Cloverly	lake	43921	1109-2	554492	CVCy1	300	5	1
Sykes Mtn	fill	43927	1110	554393	CVA23	4	5	1
Sykes Mtn	fill	43927	1110	554394	CVA23	1	5	1
Sykes Mtn	fill	43927	1110	554395	CVF9	1	5	1
Sykes Mtn	fill	43927	1110	554396	CVCo1	1	5	1
Sykes Mtn	fill	43927	1110	554397	CVA24	1	5	1
Sykes Mtn	fill	43927	1110	554398	CVA23	1	5	1
Sykes Mtn	fill	43927	1110	554399	CVA23	1	1	1
Sykes Mtn	fill	43927	1110	554399	CVCo1	23	5	1
Sykes Mtn	fill	43927	1110	554401	CVA23	1	5	1
Sykes Mtn	fill	43927	1110	554402	CVCo1	5	5	1
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Sykes Mtn	fill	43914	1205NC	554791	CVF2	3	2	1
Sykes Mtn	fill	43934	1206	554792	CVA10	1	5	1
Sykes Mtn	fill	43934	1206	554793	CVF5	1	5	1
Sykes Mtn	fill	43934	1206	554795	CVF2	1	5	1
Sykes Mtn	fill	43934	1206	554795	CVF4	1	1	1
Sykes Mtn	fill	43934	1206	554796	CVA10	1	5	1
Sykes Mtn	fill	43934	1206	554798	CVF3	1	5	1
Sykes Mtn	fill	43927	1209	554806	CVE1	1	5	1
Sykes Mtn	fill	43927	1209	554807	CVCo1	1	4	1
Sykes Mtn	fill	43927	1209	554807	CVA36	4	3	1
Sykes Mtn	fill	43927	1209	554808	CVA36	2	5	1
Sykes Mtn	fill	43927	1209	554809	CVA23	1	5	1
Sykes Mtn	fill	43927	1209	554810	CVA24	1	5	1
Sykes Mtn	fill	43927	1209	554811	CVA37	1	5	1
Sykes Mtn	fill	43914	1212	TBD0	CVA19	2	1	1
Sykes Mtn	fill	43914	1212	TBD1	CVA5	2	3	1
Sykes Mtn	fill	43914	1212	TBD2	CVF2	1	2	1
Sykes Mtn	fill	43914	1212	TBD3	CVA1	3	3	1
Sykes Mtn	fill	43914	1212	TBD4	CVA19	1	5	1
Sykes Mtn	fill	43914	1212	TBD5	CVA5	1	5	1
Sykes Mtn	fill	43914	1212	TBD6	CVA5	3	5	1
Sykes Mtn	fill	43914	1212	TBD7	CVA1	1	2	1
Sykes Mtn	fill	43914	1212	TBD8	CVA38	1	5	1
Sykes Mtn	fill	43914	1212	TBD9	CVF2	1	1	1
Sykes Mtn	fill	43914	1212	TBD10	CVA5	1	5	1
Sykes Mtn	fill	43914	1212	TBD11	CVA5	1	5	1
Sykes Mtn	fill	43914	1212	TBD12	CVA5	6	5	1
Sykes Mtn	fill	43914	1212	TBD13	CVA1	1	1	1
Sykes Mtn	fill	43914	1212	TBD14	CVF3	1	1	1
Sykes Mtn	fill	43914	1212	TBD15	CVA38	1	5	1
Sykes Mtn	fill	43914	1212	TBD16	CVA3	1	4	1
Sykes Mtn	fill	43914	1212	TBD17	CVF2	1	3	1
Sykes Mtn	fill	43914	1212	TBD18	CVA10	1	5	1
Sykes Mtn	fill	43914	1212	TBD19	CVA1	4	5	1
Sykes Mtn	fill	43914	1212	TBD20	CVF2	3	1	1
Sykes Mtn	fill	43914	1212	TBD21	CVA5	1	5	1
Sykes Mtn	fill	43914	1212	TBD22	CVF3	1	1	1
Sykes Mtn	fill	43914	1212	TBD23	CVF4	3	1	1
Sykes Mtn	fill	43914	1212	TBD24	CVA19	1	5	1
Sykes Mtn	fill	43914	1212	TBD25	CVA1	1	5	1

Sykes Mtn	fill	43914	1212	TBD26	CVA19	1	5	1
Sykes Mtn	fill	43914	1212	TBD27	CVA19	1	1	1
Sykes Mtn	fill	43914	1212	TBD28	CVA1	3	3	1
Sykes Mtn	fill	43914	1212	TBD29	CVF4	1	1	1
Sykes Mtn	fill	43914	1212	TBD30	CVF2	2	1	1
Sykes Mtn	fill	43914	1212	TBD31	CVA5	3	3	1
Sykes Mtn	fill	43914	1212	TBD32	CVF5	1	1	1
Sykes Mtn	fill	43914	1212	TBD33	CVF3	1	5	1
Sykes Mtn	fill	43914	1212	TBD34	CVF2	4	2	1
upper Cloverly	fill	43936	1216	TBD35	CVF2	4	4	1
upper Cloverly	fill	43936	1216	TBD36	CVCo1	2	1	1
upper Cloverly	fill	43936	1216	TBD37	CVA39	1	3	1
upper Cloverly	fill	43936	1216	TBD38	CVCo1	10	5	1
upper Cloverly	fill	43936	1216	TBD39	CVA39	1	5	1
upper Cloverly	fill	43936	1216	TBD40	CVCo1	3	1	1
upper Cloverly	fill	43936	1216	TBD41	CVF2	3	5	1
upper Cloverly	fill	43936	1216	TBD42	CVCo1	10	5	1
upper Cloverly	fill	43936	1216	TBD43	CVG2	1	1	1
upper Cloverly	fill	43936	1216	TBD44	CVG2	1	5	1
upper Cloverly	fill	43936	1216	TBD45	CVCo1	1	1	1
upper Cloverly	fill	43936	1216	TBD46	CVCo1	6	1	1
upper Cloverly	fill	43936	1216	TBD47	CVG2	1	4	1
upper Cloverly	fill	43936	1216	TBD48	CI2	1	3	1
upper Cloverly	fill	43936	1216	TBD49	CVF2	1	5	1
upper Cloverly	fill	43936	1216	TBD50	CVCo1	1	1	1
upper Cloverly	fill	43936	1216	TBD51	CVF2	1	5	1
upper Cloverly	fill	43936	1216	TBD52	CVCo1	3	1	1
upper Cloverly	fill	43936	1216	TBD53	CVF2	2	5	1
upper Cloverly	fill	43936	1216	TBD54	CVCo1	1	1	1
upper Cloverly	fill	43936	1216	TBD55	CVCo1	2	5	1
upper Cloverly	fill	43936	1216	TBD56	CVF2	2	1	1
upper Cloverly	fill	43936	1216	TBD57	CVA39	1	1	1
upper Cloverly	fill	43936	1216	TBD58	CVF2	1	5	1
upper Cloverly	fill	43936	1216	TBD59	CVCo1	4	1	1
upper Cloverly	fill	43936	1216	TBD60	CVCo1	3	1	1
upper Cloverly	fill	43936	1216	TBD61	CVG2	2	5	1
upper Cloverly	fill	43936	1216	TBD62	CVCo1	10	5	1
upper Cloverly	fill	43936	1216	TBD63	CVCo1	10	5	1
upper Cloverly	fill	43936	1216	TBD64	CVF2	2	5	1
upper Cloverly	fill	43936	1216	TBD65	CVCo1	2	1	1
upper Cloverly	fill	43936	1216	TBD66	CVF2	1	4	1

upper Cloverly	fill	43936	1216	TBD67	CVCo1	5	3	1
upper Cloverly	fill	43936	1216	TBD68	CVG2	1	5	1
upper Cloverly	fill	43936	1216	TBD69	CVCo1	6	5	1
upper Cloverly	fill	43936	1216	TBD70	CVCo1	25	1	1
upper Cloverly	fill	43936	1216	TBD71	CVF34	1	1	1
upper Cloverly	fill	43936	1216	TBD72	CVG2	1	5	1
upper Cloverly	fill	43936	1216	TBD73	CVCo1	2	1	1
upper Cloverly	fill	43936	1216	TBD74	CVG2	1	5	1
upper Cloverly	fill	43936	1216	TBD75	CVCo1	10	2	1
upper Cloverly	fill	43936	1216	TBD76	CVCo1	10	5	1
upper Cloverly	fill	43936	1216	TBD77	CVF2	4	5	1
upper Cloverly	fill	43936	1216	TBD78	CVCo1	1	1	1
upper Cloverly	fill	43936	1216	TBD79	CVCo1	1	5	1
upper Cloverly	fill	43936	1216	TBD80	CVCo1	3	5	1
upper Cloverly	fill	43936	1216	TBD81	CVF2	3	5	1
upper Cloverly	fill	43936	1216	TBD82	CVCo1	5	2	1
upper Cloverly	fill	43936	1216	TBD83	CVG2	1	5	1
upper Cloverly	fill	43936	1216	TBD84	CVCo1	1	5	1
upper Cloverly	fill	43936	1216	TBD85	CVCo1	4	5	1
upper Cloverly	fill	43936	1216	TBD86	CVCo1	5	5	1
upper Cloverly	fill	43936	1216	TBD87	CVCo1	6	5	1
upper Cloverly	fill	43936	1216	TBD88	CVCo1	3	5	1
upper Cloverly	fill	43936	1216	TBD89	CVF2	1	5	1
upper Cloverly	fill	43936	1216	TBD90	CVCo1	2	1	1
upper Cloverly	fill	43936	1216	TBD91	CVCo1	10	5	1
upper Cloverly	fill	43936	1216	TBD92	CVCo1	8	5	1
upper Cloverly	fill	43936	1216	TBD93	CVCo1	1	1	1
upper Cloverly	fill	43936	1216	TBD94	CVG2	1	5	1
upper Cloverly	fill	43936	1216	TBD95	CVG2	2	5	1
upper Cloverly	fill	43936	1216	TBD96	CVCo1	10	2	1
upper Cloverly	fill	43936	1216	TBD97	CVCo1	10	5	1
upper Cloverly	fill	43936	1216	TBD98	CVG2	1	2	1
upper Cloverly	fill	43936	1216	TBD99	CVCo1	1	5	1
upper Cloverly	fill	43936	1216	TBD100	CVCo1	1	5	1
upper Cloverly	fill	43936	1216	TBD101	CVCo1	1	5	1
upper Cloverly	fill	43936	1216	TBD102	CVCo1	1	5	1
upper Cloverly	fill	43936	1216	TBD103	CVCo1	5	1	1
upper Cloverly	fill	43936	1216	TBD104	CVF2	2	5	1
upper Cloverly	fill	43936	1216	TBD105	CVCo1	6	5	1
upper Cloverly	fill	43936	1216	TBD106	CVF2	1	5	1
upper Cloverly	fill	43936	1216	TBD107	CVA40	1	5	1

upper Cloverly	fill	43936	1216	TBD108	CVF2	2	2	1
upper Cloverly	fill	43936	1216	TBD109	CVCo1	10	5	1
upper Cloverly	fill	43936	1216	TBD110	CVCo1	5	1	1
upper Cloverly	fill	43936	1216	TBD111	CVG2	1	5	1
upper Cloverly	fill	43936	1216	TBD112	CVF2	2	5	1
upper Cloverly	fill	43936	1216	TBD113	CVG2	1	5	1
upper Cloverly	fill	43936	1216	TBD114	CVCo1	4	1	1
upper Cloverly	fill	43936	1216	TBD115	CVCo1	10	5	1
upper Cloverly	fill	43936	1216	TBD116	CVCo1	10	5	1
upper Cloverly	fill	43936	1216	TBD117	CVCo1	10	5	1
upper Cloverly	fill	43936	1216	TBD118	CVG2	3	3	1
upper Cloverly	fill	43936	1216	TBD119	CVCo1	10	4	1
upper Cloverly	fill	43936	1216	TBD120	CVG2	1	5	1
upper Cloverly	fill	43936	1216	TBD121	CVCo1	10	2	1
upper Cloverly	fill	43936	1216	TBD122	CVF2	1	5	1
upper Cloverly	fill	43936	1216	TBD123	CVA39	1	5	1
Sykes Mtn	fill	43932	11PP1	554499	CVCo1	9	5	1
Sykes Mtn	fill	43932	11PP1	554500	CVCo1	1	5	1
Sykes Mtn	fill	43914	11PP3	554501	CVA1	2	5	1
Sykes Mtn	fill	43914	11PP3	554501	CVF2	2	1	1
Sykes Mtn	fill	43914	11PP3	554502	CVA1	3	5	1
Sykes Mtn	fill	43914	11PP3	554502	CVF2	1	1	1
Sykes Mtn	fill	43928	11PP6	554503	CVA10	1	5	1
Sykes Mtn	fill	43928	11PP6	554504	CVCo1	10	5	1
Sykes Mtn	fill	43928	11PP6	554506	CVCo1	9	5	1
Sykes Mtn	fill	43928	11PP6	554507	CVCo1	7	5	1
Sykes Mtn	fill	43928	11PP6	554508	CVCo1	6	5	1
lower Cloverly	lake	43908	11PP7	554509	CVCy1	20	5	1
lower Cloverly	lake	43908	11PP7	554510	CVCy1	1	4	1
lower Cloverly	lake	43908	11PP7	554510	CVF1	1	3	1
lower Cloverly	lake	43908	11PP7	554511	CVF1	1	5	1
Sykes Mtn	fill	43919	11PP8	554512	CVF4	1	3	1
Sykes Mtn	fill	43919	11PP8	554512	CVCo1	1	4	1
Sykes Mtn	fill	43919	11PP8	554514	CVCo1	1	5	1
Sykes Mtn	fill	43919	11PP8	554515	CVCo1	2	5	1
Sykes Mtn	fill	43919	11PP8	554516	CVCo1	4	5	1
Sykes Mtn	fill	43919	11PP8	554517	CVF4	1	5	1
Sykes Mtn	fill	43919	11PP8	554517	CVCo1	1	2	1
lower Cloverly	fill	43922	11PP9	554524	CVF40	4	5	1
lower Cloverly	fill	43922	11PP9	554525	CVCo7	1	5	1
lower Cloverly	fill	43922	11PP9	554525	CVI1	5	1	1

lower Cloverly	fill	43922	11PP9	554526	CVI1	5	5	1
lower Cloverly	fill	43922	11PP9	554527	CVI1	4	5	1
lower Cloverly	fill	43922	11PP9	554528	CVI1	6	5	1
lower Cloverly	fill	43922	11PP9	554529	CVI1	10	5	1
lower Cloverly	fill	43922	11PP9	554530	CVI1	7	5	1
lower Cloverly	fill	43922	11PP9	554531	CVF41	1	1	1
lower Cloverly	fill	43922	11PP9	554531	CVCo7	1	5	1
lower Cloverly	lake	43938	11PP9 upper	554521	CVF19	1	5	1
lower Cloverly	lake	43938	11PP9 upper	554521	CVF18	1	1	1
lower Cloverly	lake	43938	11PP9 upper	554520	CVF19	1	5	1
lower Cloverly	lake	43938	11PP9 upper	554520	CVF13	2	1	1
lower Cloverly	lake	43938	11PP9 upper	554519	CVF19	2	5	1
lower Cloverly	lake	43923	11PP12	554533	CVF19	2	4	1
lower Cloverly	lake	43923	11PP12	554533	CVF1	1	2	1
lower Cloverly	lake	43923	11PP12	554534	CVCy1	1	5	1
lower Cloverly	lake	43923	11PP12	554535	CVF18	6	5	1
lower Cloverly	lake	43923	11PP12	554535	CVF1	1	2	1
lower Cloverly	lake	43923	11PP12	554536	CVF18	1	3	1
lower Cloverly	lake	43923	11PP12	554536	CVF14	1	3	1
lower Cloverly	lake	43923	11PP12	554537	CVF1	1	3	1
lower Cloverly	lake	43923	11PP12	554537	CVF14	3	4	1
lower Cloverly	lake	43923	11PP12	554537	CVF19	1	1	1
lower Cloverly	lake	43923	11PP12	554538	CVF1	1	4	1
lower Cloverly	lake	43923	11PP12	554538	CVF20	1	3	1
lower Cloverly	lake	43923	11PP12	554539	CVF19	1	5	1
lower Cloverly	lake	43923	11PP12	554540	CVF19	4	2	1
lower Cloverly	lake	43923	11PP12	554540	CVF1	2	2	1
lower Cloverly	lake	43923	11PP12	554540	CVF14	6	4	1
lower Cloverly	fill	43925	11PP18	554588	CVI1	100	5	1
lower Cloverly	fill	43925	11PP18	554590	CVI1	4	5	1
lower Cloverly	fill	43925	11PP18	554590	CVI1	5	3	1
lower Cloverly	fill	43925	11PP18	554590	CVCy3	1	4	1
lower Cloverly	fill	43925	11PP18	554591	CVCy3	1	5	1
lower Cloverly	fill	43925	11PP18	554592	CVF17	1	1	1
lower Cloverly	fill	43925	11PP18	554592	CVG1	1	4	1
lower Cloverly	fill	43925	11PP18	554592	CVI1	4	1	1
lower Cloverly	fill	43925	11PP18	554592	CVCy3	1	3	1
lower Cloverly	fill	43925	11PP18	554593	CVCy3	1	4	1

lower Cloverly	fill	43925	11PP18	554593	CVI1	3	3	1
lower Cloverly	fill	43926	11PP19	554594	CVF1	1	5	1
lower Cloverly	fill	43926	11PP19	554595	CVF42	2	5	1
lower Cloverly	fill	43926	11PP19	554596	CVE1	2	5	1
lower Cloverly	fill	43926	11PP19	554597	CVG1	1	5	1
lower Cloverly	fill	43926	11PP19	554598	CVE1	2	5	1
lower Cloverly	fill	43926	11PP19	554599	CVF42	2	4	1
lower Cloverly	fill	43926	11PP19	554599	CVF45	1	3	1
lower Cloverly	fill	43926	11PP19	554601	CVF44	1	1	1
lower Cloverly	fill	43926	11PP19	554601	CVE1	2	5	1
lower Cloverly	fill	43926	11PP19	554602	CVF1	1	5	1
lower Cloverly	fill	43926	11PP19	554602	CVF44	1	1	1
lower Cloverly	fill	43926	11PP19	554603	CVF43	1	1	1
lower Cloverly	fill	43926	11PP19	554603	CVE1	4	5	1
lower Cloverly	fill	43926	11PP19	554604	CVE1	1	5	1
lower Cloverly	fill	43926	11PP19	554605	CVI1	3	1	1
lower Cloverly	fill	43926	11PP19	554606	CVE1	4	5	1
lower Cloverly	fill	43926	11PP19	554607	CVF1	2	4	1
lower Cloverly	fill	43926	11PP19	554607	CVE1	1	3	1
lower Cloverly	fill	43926	11PP19	554607	CVI1	3	1	1
lower Cloverly	fill	43926	11PP19	554608	CVE1	1	4	1
lower Cloverly	fill	43926	11PP19	554608	CVF42	1	3	1
lower Cloverly	fill	43926	11PP19	554611	CVE1	2	5	1
lower Cloverly	fill	43926	11PP19	554612	CVF46	1	5	1
lower Cloverly	fill	43926	11PP19	554613	CVF45	2	5	1
lower Cloverly	fill	43926	11PP19	554614	CVE1	1	4	1
lower Cloverly	fill	43926	11PP19	554614	CVF42	1	3	1
lower Cloverly	fill	43926	11PP19	554614	CVI1	1	1	1
lower Cloverly	fill	43926	11PP19	554615	CVE1	1	4	1
lower Cloverly	fill	43926	11PP19	554615	CVF42	1	3	1
lower Cloverly	fill	43926	11PP19	554616	CVF45	1	1	1
lower Cloverly	fill	43926	11PP19	554616	CVI1	12	5	1
lower Cloverly	fill	43926	11PP19	554617	CVF42	1	1	1
lower Cloverly	fill	43926	11PP19	554617	CVE1	5	5	1
lower Cloverly	fill	43926	11PP19	554618	CVE1	5	5	1
lower Cloverly	fill	43926	11PP19	554618	CVF1	3	1	1
lower Cloverly	fill	43926	11PP19	554619	CVE1	3	5	1
lower Cloverly	fill	43926	11PP19	554619	CVF1	1	1	1
lower Cloverly	fill	43926	11PP19	554619	CVF43	1	1	1
lower Cloverly	fill	43926	11PP19	554620	CVF42	1	5	1
lower Cloverly	fill	43926	11PP19	554620	CVE1	1	2	1

lower Cloverly	fill	43926	11PP19	554621	CVF1	3	5	1
lower Cloverly	fill	43926	11PP19	554621	CVI1	1	1	1
lower Cloverly	fill	43926	11PP19	554622	CVCo8	1	5	1
lower Cloverly	fill	43926	11PP19	554523	CVF42	1	5	1
lower Cloverly	fill	43926	11PP19	554624	CVF1	1	4	1
lower Cloverly	fill	43926	11PP19	554625	CVF42	1	5	1
lower Cloverly	fill	43926	11PP19	554627	CVE1	2	5	1
lower Cloverly	fill	43926	11PP19	554627	CVF47	1	1	1
lower Cloverly	fill	43926	11PP19	554528	CVF42	1	4	1
lower Cloverly	fill	43926	11PP19	554528	CVI1	1	3	1
lower Cloverly	fill	43926	11PP19	554529	CVE1	1	5	1
lower Cloverly	fill	43926	11PP19	NA1	CVE1	1	5	1
lower Cloverly	fill	43926	11PP19	NA2	CVE1	1	5	1
lower Cloverly	fill	43926	11PP19	NA3	CVE1	1	5	1
lower Cloverly	fill	43926	11PP19	NA4	CVE1	1	5	1
lower Cloverly	fill	43926	11PP19	NA5	CVE1	1	5	1
lower Cloverly	fill	43926	11PP19	NA6	CVE1	1	5	1
lower Cloverly	fill	43926	11PP19	NA7	CVE1	1	5	1
lower Cloverly	fill	43926	11PP19	NA8	CVE1	1	5	1
lower Cloverly	fill	43926	11PP19	NA9	CVE1	1	5	1
lower Cloverly	fill	43926	11PP19	NA10	CVE1	1	5	1
lower Cloverly	fill	43926	11PP19	NA11	CVE1	1	5	1
lower Cloverly	fill	43926	11PP19	NA12	CVE1	1	5	1
lower Cloverly	fill	43926	11PP19	NA13	CVE1	1	5	1
lower Cloverly	fill	43926	11PP19	NA14	CVE1	1	5	1
lower Cloverly	fill	43926	11PP19	NA15	CVE1	1	5	1
lower Cloverly	fill	43926	11PP19	NA16	CVE1	1	5	1
lower Cloverly	fill	43926	11PP19	NA17	CVE1	1	5	1
lower Cloverly	fill	43926	11PP19	NA18	CVE1	1	5	1
lower Cloverly	fill	43926	11PP19	NA19	CVE1	1	5	1
lower Cloverly	fill	43926	11PP19	NA20	CVE1	1	5	1
lower Cloverly	fill	43926	11PP19	NA21	CVE1	1	5	1
lower Cloverly	fill	43926	11PP19	NA22	CVE1	1	5	1
lower Cloverly	fill	43926	11PP19	NA23	CVE1	1	5	1
lower Cloverly	fill	43926	11PP19	NA24	CVE1	1	5	1
lower Cloverly	fill	43926	11PP19	NA25	CVE1	1	5	1
lower Cloverly	fill	43926	11PP19	NA26	CVE1	1	5	1
lower Cloverly	fill	43926	11PP19	NA27	CVE1	1	5	1
lower Cloverly	fill	43926	11PP19	NA28	CVE1	1	5	1
lower Cloverly	fill	43926	11PP19	NA29	CVE1	1	5	1
lower Cloverly	fill	43926	11PP19	NA30	CVE1	1	5	1

lower Cloverly	fill	43926	11PP19	NA31	CVE1	1	5	1
lower Cloverly	fill	43926	11PP19	NA32	CVE1	1	5	1
lower Cloverly	fill	43926	11PP19	NA33	CVE1	1	5	1
lower Cloverly	fill	43926	11PP19	NA34	CVE1	1	5	1
lower Cloverly	fill	43926	11PP19	NA35	CVE1	1	5	1

Appendix III

Morphotype abundance data used in Chapter 5.

Counts of plant morphotype abundance at eleven sites using three different methods. Note slight differences in rank order abundance between methods.

Collection NAJ 1102: Comparison of three measures of abundance

	Relative Abundance of Plant Morphotypes		
Morphotype	Fragments	Braun-Blanquet	Quadrats
CVA1	512	258	56
CVF2	233	69	49
CVF4	72	50	30
CVF3	38	22	22
CVCo1	27	15	7
CVA2	21	12	11
CVF5	5	6	5
CVA3	5	5	5
CVF25	2	3	2
CVA18	1	3	1
CVA5	1	2	1
CVF26	1	2	1
CVF22	1	1	1

Collection NAJ1103 Comparison of three measures of abundance

	Relative Abundance of Plant Morphotypes		
Morphotype	Fragments	Braun-Blanquet	Quadrats
CVCo1	207	140	35
CVA3	42	49	18
CVA20	10	31	9
CVA11	6	23	6
CVF26	9	13	5
CVF4	4	6	4
CVA5	2	9	2
CVA21	1	5	1
CVA22	1	5	1
CVF2	1	5	1
CVF27	1	3	1
CVF28	1	3	1

Collection NAJ1105: Comparison of three measures of abundance

	Relative Abundance of Plant Morphotypes		
Morphotype	Fragments	Braun-Blanquet	Quadrats

Collection NAJ1107: Comparison of three measures of abundance

	Relative Abundance of Plant Morphotypes		
Morphotype	Fragments	Braun-Blanquet	Quadrats
CVCo1	170	178	41
CVF4	32	66	17
CVA24	3	10	2

Collection NAJ 1108: Comparison of three measures of abundance

	Relative Abundance of Plant Morphotypes		
Morphotype	Fragments	Braun-Blanquet	Quadrats
CVF1	16	37	13
CVI1	46	34	11
CVCy1	30	31	7
CVCo6	7	13	5
CVCo2	5	9	4
CVF19	4	12	4
CVCo4	3	7	3
CVF13	3	5	2
CVF15	2	4	2
CVCy2	2	4	1
CVCo3	1	5	1
CVF16	1	4	1

Collection NAJ1110: Comparison of three measures of abundance

	Relative Abundance of Plant Morphotypes		
Morphotype	Fragments	Braun-Blanquet	Quadrats
CVCo1	86	102	27
CVA23	24	79	18
CVA24	13	59	12
CVF4	12	39	9
CVF30	3	13	3
CVF31	2	8	2
CVF2	3	4	1
CVA25	1	4	1
CVF7	1	3	1

Collection NAJ 11PP09: Comparison of three measures of abundance

	Relative Abundance of Plant Morphotypes		
Morphotype	Fragments	Braun-Blanquet	Quadrats
CVI1	17	10	2
CVF40	6	10	12
CVF41	5	6	2
CVF19	3	10	12
CVF13	3	6	2
CVF14	3	2	2
CVCo7	2	10	2

Collection NAJ11PP18: Comparison of three measures of abundance

	Relative Abundance of Plant Morphotypes		
Morphotype	Fragments	Braun-Blanquet	Quadrats
CVI1	116	17	5
CVCy3	4	16	4
CVG1	1	4	1
CVF13	1	1	1

Collection NAJ11PP19: Comparison of three measures of abundance

	Relative Abundance of Plant Morphotypes		
Morphotype	Fragments	Braun-Blanquet	Quadrats
CVE1	73	252	52
CVF42	12	38	10
CVF1	12	25	7
CVI1	21	12	6
CVF45	4	9	3
CVF43	2	2	2
CVF44	2	2	2
CVCo8	1	5	1
CVF46	1	5	1
CVG1	1	5	1
CVF47	1	1	1

Collection NAJ1204: Comparison of three measures of abundance

	Relative Abundance of Plant Morphotypes		
Morphotype	Fragments	Braun-Blanquet	Quadrats
CVF2	41	64	17
CVF4	17	15	10
CVCo1	13	19	8
CVA10	10	27	10
CVF3	8	12	4
CVF33	8	10	4
CVF7	5	11	3
CVA30	2	10	2
CVA29	1	5	1
CVA31	1	5	1
CVA33	1	5	1
CVA34	1	4	1
CVA32	1	1	1

Collection NAJ1216: Comparison of three measures of abundance

	Relative Abundance of Plant Morphotypes		
Morphotype	Fragments	Braun-Blanquet	Quadrats
CVCo1	280	163	50
CVF2	33	76	17
CVG2	19	65	15
CVA39	1	5	1
CVI2	1	3	1
CVF34	1	1	1

Appendix IV

Attributes of the plant fossil collections from the Cloverly and Sykes Mountain formations. Some collections were made from the same USNM localities and therefore had the same attributes. Sites were scored for stratigraphic position, geographic location, and sedimentological features. Sedimentological features were used to interpret depositional environment category.

Collection Attributes										
collection	USNM locality	type	unit	latitude	longitude	geometry	grain size	bedding	color	depositional environment
1001	43903	prospect	Sykes Mtn	44.5241383	-108.014555	?	sand-silt	cross lam	light brown	splay
1002	43903	prospect	Sykes Mtn	44.5241383	-108.014555	?	sand	cross lam	light brown	splay
1004	43904	census	Sykes Mtn	44.967611	108.3081638	extensive	sand	massive	light gray	splay
1012	43904	prospect	Sykes Mtn	44.967611	108.3081638	extensive	sand	massive	light gray	splay
1006	43906	prospect	Sykes Mtn	?	?	lenticular	silt	flat lam	brown	fill
1007	43907	prospect	Sykes Mtn	44.5241389	-108.0148055	lenticular	silt	flat lam	gray	fill
1203	43907	prospect	Sykes Mtn	44.5241389	-108.0148055	lenticular	silt	flat lam	gray	fill
11PP8	43907	prospect	Sykes Mtn	44.5241389	-108.0148055	lenticular	silt	flat lam	gray	fill
1009	43909	prospect	Sykes Mtn	?	?	?	silt	cross lam	gray	?
1010	43910	prospect	Sykes Mtn	44.5059722	-107.856972	lenticular	silt	flat lam	brown	fill
1011	43935	prospect	Sykes Mtn	44.9676	108.30816	extensive	silt	ripple lam	gray-green	fill
1013	43911	census	lower Cloverly	44.0411667	-107.5078056	lenticular	silt	flat lam	light brown	fill
1101	43913	census	Sykes Mtn	44.523	-108.0160833	lenticular	sand	flat lam/ massive	gray	splay

1102	43914	census	Sykes Mtn	44.50975	-107.86175	lenticular	silt	flat lam	brown-gray	fill
1205	43914	prospect	Sykes Mtn	44.50975	-107.86175	lenticular	silt	flat lam	brown-gray	fill
1212	43914	prospect	Sykes Mtn	44.50975	-107.86175	lenticular	silt	flat lam	brown-gray	fill
1102NC	43914	prospect	Sykes Mtn	44.50975	-107.86175	lenticular	silt	flat lam	brown-gray	fill
11PP3	43914	prospect	Sykes Mtn	44.50975	-107.86175	lenticular	silt	flat lam	brown-gray	fill
1205NC	43914	prospect	Sykes Mtn	44.50975	-107.86175	lenticular	silt	flat lam	brown-gray	fill
1103	43915	census	Sykes Mtn	44.967	-108.30625	lenticular	silt	flat lam	gray	fill
1104	43916	prospect	Sykes Mtn	44.96833333	-108.3085	extensive	silt	ripple lam	gray-green	fill
1105	43917	census	Sykes Mtn	44.96766667	-108.30825	extensive	sand	flat lam/ massive	gray	splay
1106	43918	prospect	Sykes Mtn	44.967	-108.30625	extensive	sand	massive/ flat lam	gray	splay
1107	43919	census	Sykes Mtn	44.032	-107.5095833	lenticular	sandy silt	flat lam	light brown	fill
1110	43927	census	Sykes Mtn	44.03258333	-107.5160833	lenticular	silt	flat lam	brown	fill
1209	43927	prospect	Sykes Mtn	44.03258333	-107.5160833	lenticular	silt	flat lam	brown	fill
1111	43910	prospect	Sykes Mtn	44.5059722	-107.856972	lenticular	silt	flat lam	brown	fill
1201	43933	prospect	Sykes Mtn	?	?	lenticular	silt	flat lam	brown-gray	fill
1204	43934	census	Sykes Mtn	44.512195	-107.897245	lenticular	silt	flat lam	brown	fill
1204Pitt	43934	prospect	Sykes Mtn	44.512195	-107.897245	lenticular	silt	flat lam	brown	fill
1206	43934	prospect	Sykes Mtn	?	?	lenticular	silt	flat lam	brown	fill
1216	43936	census	upper Cloverly	44.98448	-108.330135	lenticular	silt	flat lam	gray	fill

11PP1	43932	prospect	upper Cloverly	44.52383333	-108.0158333	lenticular	clay	massive	light gray	fill
11PP18	43925	census	lower Cloverly	44.0805283	-107.535513	lenticular	silt	flat lam	brown	fill
11PP19	43926	census	lower Cloverly	44.080715	-107.535565	lenticular	silt	flat lam	brown	fill
11PP6	43928	prospect	Sykes Mtn	44.96725	-108.3071667	lenticular	silt	flat lam	gray	fill
11PP9	43922	prospect	lower Cloverly	44.03458333	-107.5143333	lenticular	silt	flat lam	gray	fill
1008	43908	prospect	lower Cloverly	44.035	-107.5068	extensive	silt	flat lam	gray	lake
1108	43920	census	lower Cloverly	44.03341667	-107.5155	extensive	silt	flat lam	gray	lake
1109	43921	prospect	lower Cloverly	44.0365	-107.516	extensive	silt	flat lam	gray	lake
1109-1	43921	prospect	lower Cloverly	44.0365	-107.516	extensive	silt	flat lam	gray	lake
1109-2	43921	prospect	lower Cloverly	44.0365	-107.516	extensive	silt	flat lam	gray	lake
11PP12	43923	prospect	lower Cloverly	44.0365	-107.50775	extensive	silt	flat lam	gray	lake
11PP14	43912	prospect	lower Cloverly	44.035525	-107.517795	extensive	silt	flat lam	gray	lake
11PP7	43908	prospect	lower Cloverly	44.035	-107.5074167	extensive	silt	flat lam	gray	lake
11PP9 upper	43922	prospect	lower Cloverly	44.03458333	-107.5143333	extensive	silt	flat lam	gray	lake
SLWPP1004	43912	prospect	lower Cloverly	44.035525	-107.517795	extensive	silt	flat lam	gray	lake

Appendix V

Data Matrix from Museum Collections and literature sources.

Summary data for the Lower Cretaceous collections from the United States												
Unique ID	Lat.	Long.	effort	richness	FPs	energy	age	bin	lower Ma	upper Ma	Coll. reference	Age ref.
1	47.4833	-111.367	2	14	0	low	early Albian	3	-113	-109	Lapasha 1983	Vuke, 2000
2	47.4833	-111.367	1	7	0	low	early Albian	3	-113	-109	Lapasha 1983	Vuke, 2000
3	47.4833	-111.367	1	4	0	low	early Albian	3	-113	-109	Lapasha 1983	Vuke, 2000
4	47.4833	-111.367	1	2	0	low	early Albian	3	-113	-109	Lapasha 1983	Vuke, 2000
5	47.4833	-111.367	1	4	0	low	early Albian	3	-113	-109	Lapasha 1983	Vuke, 2000
6	47.4833	-111.367	2	7	0	low	early Albian	3	-113	-109	Lapasha 1983	Vuke, 2000
7	47.4833	-111.367	1	4	0	low	early Albian	3	-113	-109	Lapasha 1983	Vuke, 2000
8	47.4833	-111.367	2	13	0	low	early Albian	3	-113	-109	Lapasha 1983	Vuke, 2000
9	47.4833	-111.367	2	16	0	low	early Albian	3	-113	-109	Lapasha 1983	Vuke, 2000
10	47.4833	-111.367	2	7	0	low	early Albian	3	-113	-109	Lapasha 1983	Vuke, 2000
11	47.4833	-111.367	1	1	0	low	early Albian	3	-113	-109	Lapasha 1983	Vuke, 2000
12	47.4833	-111.367	1	3	0	low	early Albian	3	-113	-109	Lapasha 1983	Vuke, 2000
13	47.4833	-111.367	1	2	0	low	early Albian	3	-113	-109	Lapasha 1983	Vuke, 2000

14	47.4833	-111.367	1	6	0	low	early Albian	3	-113	-109	Lapasha 1983	Vuke, 2000
15	47.4833	-111.367	1	3	0	low	early Albian	3	-113	-109	Lapasha 1983	Vuke, 2000
16	47.4833	-111.367	2	8	0	low	early Albian	3	-113	-109	Lapasha 1983	Vuke, 2000
17	47.4833	-111.367	1	6	0	low	early Albian	3	-113	-109	Lapasha 1983	Vuke, 2000
18	47.4833	-111.367	1	3	0	low	early Albian	3	-113	-109	Lapasha 1983	Vuke, 2000
19	47.4833	-111.367	1	8	0	low	early Albian	3	-113	-109	Lapasha 1983	Vuke, 2000
20	47.4833	-111.367	1	5	0	low	early Albian	3	-113	-109	Lapasha 1983	Vuke, 2000
21	47.4833	-111.367	3	18	0	low	early Albian	3	-113	-109	Lapasha 1983	Vuke, 2000
22	47.4833	-111.367	1	10	0	low	early Albian	3	-113	-109	Lapasha 1983	Vuke, 2000
23	47.4833	-111.367	1	11	0	low	early Albian	3	-113	-109	Lapasha 1983	Vuke, 2000
24	47.4833	-111.367	1	6	0	low	early Albian	3	-113	-109	Lapasha 1983	Vuke, 2000
25	47.4833	-111.367	3	18	1	low	early Albian	3	-113	-109	Lapasha 1983	Vuke, 2000
26	47.4833	-111.367	1	7	0	low	early Albian	3	-113	-109	Lapasha 1983	Vuke, 2000
27	47.4833	-111.367	1	9	0	low	early Albian	3	-113	-109	Lapasha 1983	Vuke, 2000
28	47.4833	-111.367	1	5	0	low	early Albian	3	-113	-109	Lapasha 1983	Vuke, 2000
29	47.4833	-111.367	1	9	0	low	early Albian	3	-113	-109	Lapasha 1983	Vuke, 2000
30	47.4833	-111.367	2	10	0	low	early Albian	3	-113	-109	Lapasha 1983	Vuke, 2000
31	47.4833	-111.367	1	2	0	low	early Albian	3	-113	-109	Lapasha 1983	Vuke, 2000
32	47.4833	-111.367	1	9	0	low	early Albian	3	-113	-109	Lapasha 1983	Vuke, 2000

33	47.4833	-111.367	3	20	0	low	early Albian	3	-113	-109	Lapasha 1983	Vuke, 2000
34	47.4833	-111.367	1	5	0	low	early Albian	3	-113	-109	Lapasha 1983	Vuke, 2000
35	47.4833	-111.367	3	21	0	low	early Albian	3	-113	-109	Lapasha 1983	Vuke, 2000
36	47.4833	-111.367	1	3	0	low	early Albian	3	-113	-109	Lapasha 1983	Vuke, 2000
37	47.4833	-111.367	1	6	0	low	early Albian	3	-113	-109	Lapasha 1983	Vuke, 2000
38	47.4833	-111.367	1	2	0	low	early Albian	3	-113	-109	Lapasha 1983	Vuke, 2000
39	47.4833	-111.367	1	5	0	low	early Albian	3	-113	-109	Lapasha 1983	Vuke, 2000
40	47.4833	-111.367	1	1	0	low	early Albian	3	-113	-109	Lapasha 1983	Vuke, 2000
41	47.4833	-111.367	2	7	0	low	early Albian	3	-113	-109	Lapasha 1983	Vuke, 2000
42	47.4833	-111.367	3	15	0	low	early Albian	3	-113	-109	Lapasha 1983	Vuke, 2000
43	47.4833	-111.367	1	4	0	low	early Albian	3	-113	-109	Lapasha 1983	Vuke, 2000
44	47.4833	-111.367	1	2	0	low	early Albian	3	-113	-109	Lapasha 1983	Vuke, 2000
45	47.4833	-111.367	1	4	0	low	early Albian	3	-113	-109	Lapasha 1983	Vuke, 2000
46	47.4833	-111.367	3	17	0	low	early Albian	3	-113	-109	Lapasha 1983	Vuke, 2000
47	47.4833	-111.367	2	11	0	low	early Albian	3	-113	-109	Lapasha 1983	Vuke, 2000
48	47.4833	-111.367	2	9	0	low	early Albian	3	-113	-109	Lapasha 1983	Vuke, 2000
49	42.08	-110.16	1	1	1	low	mid-late Albian	4	-109	-100.5	Peppe et al. 2008	Peppe et al. 2008
50	42.08	-110.16	1	4	1	low	mid-late Albian	4	-109	-100.5	Peppe et al. 2008	Peppe et al. 2008
51	42.08	-110.16	2	9	1	low	mid-late Albian	4	-109	-100.5	Peppe et al. 2008	Peppe et al. 2008
52	42.08	-110.16	2	17	2	low	mid-late Albian	4	-109	-100.5	Peppe et al. 2008	Peppe et al. 2008

53	42.08	-110.16	2	14	2	low	mid-late Albian	4	-109	-100.5	Peppe et al. 2008	Peppe et al. 2008
54	42.08	-110.16	3	13	1	low	mid-late Albian	4	-109	-100.5	Brown 1933	Peppe et al. 2008
55	37.45	-99.07	2	4	1	high	early late Albian	4	-105	-100.5	Berry 1922	
56	37.45	-99.07	2	2	2	high	early late Albian	4	-105	-100.5	Berry 1922	
57	37.45	-99.07	2	4	1	high	early late Albian	4	-105	-100.5	Berry 1922	
58	37.45	-99.07	2	3	1	high	early late Albian	4	-105	-100.5	Berry 1922	
59	37.45	-99.07	2	2	2	high	early late Albian	4	-105	-100.5	Berry 1922	
60	37.45	-99.07	2	5	2	high	early late Albian	4	-105	-100.5	Berry 1922	
61	37.45	-99.07	2	3	1	high	early late Albian	4	-105	-100.5	Berry 1922	
62	37.45	-99.07	2	1	0	high	early late Albian	4	-105	-100.5	Berry 1922	
63	37.45	-99.07	2	8	1	high	early late Albian	4	-105	-100.5	Berry 1922	
64	37.45	-99.07	2	3	1	high	early late Albian	4	-105	-100.5	Berry 1922	
65	37.45	-99.07	2	2	0	high	early late Albian	4	-105	-100.5	Berry 1922	
66	37.45	-99.07	2	1	0	high	early late Albian	4	-105	-100.5	Berry 1922	
67	37.45	-99.07	2	2	1	high	early late Albian	4	-105	-100.5	Berry 1922	
68	37.45	-99.07	2	6	2	high	early late Albian	4	-105	-100.5	Berry 1922	
69	37.45	-99.07	2	3	2	high	early late Albian	4	-105	-100.5	Berry 1922	
70	37.45	-99.07	2	3	1	high	early late Albian	4	-105	-100.5	Berry 1922	
71	37.45	-99.07	2	2	2	high	early late Albian	4	-105	-100.5	Berry 1922	
72	37.45	-99.07	2	2	1	high	early late Albian	4	-105	-100.5	Berry 1922	
73	37.45	-99.07	2	1	2	high	early late Albian	4	-105	-100.5	Berry 1922	
74	37.45	-99.07	2	3	1	high	early late Albian	4	-105	-100.5	Berry 1922	
75	37.466	-99.11	3	16	1	high	early late Albian	4	-105	-100.5	Huang and Dilcher 1994	
76	38.196	-108.585	2	9	1	low	early Cenomanian	4	-100.5	-97	Brown 1950	
77	38.189	-108.64	2	14	2	low	early Cenomanian	4	-100.5	-97	Brown 1950	
78	38.249	-	3	5	0	low	early Cenomanian	4	-100.5	-97	Brown 1950	

		108.674										
79	39.146	-109.14	3	19	1	low	early Cenomanian	4	-100.5	-97	Rushforth 1971	
80	44.2748	-94.3868	3	28	2	low	Cenomanian	4	-101	-95	Wang and Dilcher 2009	
81	39.3068	-97.5677	3	31	2	low	Cenomanian	4	-101	-95	Wang and Dilcher 2010	
82	40.05	-97.1688	3	35	2	low	Cenomanian	4	-101	-95	Wang and Dilcher 2011	
83	38.2506	-108.6	1	1	0	low	Aptian	1	-145	-105	Brown 1950	
84	34.0822	-93.8475	3	1	0	low	Aptian	2	-125	-113	Axsmith et al. 2004	Axsmith et al. 2004
85	47.45	-103.6	1	1	0	low	Neocomian-Aptian	1	-145	-119	Ward 1905	Post and Bell, 1961
86	32.326	-97.798	3	1	0	high	Aptian	3	-112	-110	Axsmith and Jacobs 2005	Jacobs et al. 1991
87	43.425	-103.794	1	8	0	high	Aptian	1	-134	-119	Cahoon 1960	Post and Bell, 1961
88	38.494	-77.341	3	22	1	low	mid-late Albian	4	-106	-101	Upchurch et al. 1994	Hochuli et al. 2006
89	32.54	-100.2	2	7	1	low	mid-late Albian	4	-105	-102	Serlin 1982	Mancini and Scott 2006
90	32.3	-98.25	1	3	2	low	mid-late Albian	3	-108	-105	Ball 1937	Mancini and Scott 2006
91	47.18	-110.582	1	4	0	low	Aptian-early Albian	2	-125	-109		Vuke, 2000
92	47.18	-110.582	3	12	0	low	Aptian-early Albian	2	-125	-109	Knowlton 1907; Fisher 1909	Vuke, 2000
93	47.3	-111.86	1	4	0	high	Aptian-early Albian	2	-125	-109	Knowlton 1907; Fisher 1909	Vuke, 2000
94	47.18	-110.582	1	7	0	low	Aptian-early Albian	2	-125	-109	Knowlton 1907; Fisher 1909	Vuke, 2000
95	47.218	-111.347	1	6	0	low	Aptian-early Albian	2	-125	-109	Knowlton 1907; Fisher 1909	Vuke, 2000
96	47.3	-111.86	1	3	0	mod	Aptian-early Albian	2	-125	-109	Fisher 1909	Vuke, 2000
97	47.54	111.445	2	5	0	mod	Aptian-early Albian	2	-125	-109	Fontaine 1892	Vuke, 2000
98	47.54	111.445	1	3	0	low	Aptian-early Albian	2	-125	-109	Fontaine 1892	Vuke, 2000
99	47.54	111.445	1	1	0	low	Aptian-early Albian	2	-125	-109	Fontaine 1892	Vuke, 2000
100	47.379	-110.922	3	15	0	low	pre-Aptian	1	-150	-125		

101	45.06	-111.28	2	7	0	low	late Albian	4	-104	-101	Vuke in prep	Oboh-Ikuenobe et al. 2007
102	43	-112	1	NA	1		Albian	4	-105	-95	Crabtree 1983	Crabtree 1987
103	39.5	-115.93	1	4	0	low	Aptian	2	-125	-113	J. Paleo 1941	
104	39.5	-115.93	2	7	0	low	Aptian	2	-125	-113	McNeil, 1939	
105	44.65	-104.217	1	2	0	low	mid Albian	3	-109	-105		Post and Bell, 1961
106	44.65	-104.217	1	3	0	mod	mid Albian	3	-109	-105		Post and Bell, 1961
107	44.65	-104.217	3	7	1	mod	mid Albian	3	-109	-105	Ward et al. 1899	Post and Bell, 1961
108	44.65	-104.217	3	8	2	mod	mid Albian	3	-109	-105	Ward et al. 1899	Post and Bell, 1961
109	44.59	-104.04	1	2	0	low	Neocomian-Aptian	1	-145	-113	Ward	Post and Bell, 1961
110	44.65	-104.217	1	4	0	mod	mid Albian	3	-109	-105	Ward et al. 1899	Post and Bell, 1961
111	44.65	-104.217	1	4	0	low	mid Albian	3	-109	-105	Ward et al. 1899	Post and Bell, 1961
112	44.65	-104.217	1	4	0	mod	mid Albian	3	-109	-105	Ward et al. 1899	Post and Bell, 1961
113	44.65	-104.217	1	3	0	low	Aptian-early Albian	3	-119	-109	Ward et al. 1899	Post and Bell, 1961
114	44.65	-104.217	1	1	0	low	mid Albian	3	-109	-105	Ward et al. 1899	Post and Bell, 1961
115	44.65	-104.217	1	4	0	mod	Aptian-early Albian	3	-119	-109	Ward et al. 1899	Post and Bell, 1961
116	44.65	-104.217	1	4	2	mod	mid Albian	3	-109	-105	Ward et al. 1899	Post and Bell, 1961
117	44.61	-104.13	1	3	0	low	Neocomian-Aptian	1	-145	-113	Ward	Post and Bell, 1961
118	44.65	-104.217	1	2	0	mod	mid Albian	3	-109	-105	Ward et al. 1899	Post and Bell, 1961
119	44.65	-104.217	1	3	0	low	Aptian-early Albian	3	-119	-109	Ward et al. 1899	Post and Bell, 1961
120	44.65	-104.217	1	1	0	low	mid Albian	3	-109	-105	Ward et al. 1899	Post and Bell, 1961
121	44.62	-104.1	1	2	0	mod	Neocomian-Aptian	1	-145	-113	Ward	Post and Bell, 1961

122	44.63	-104.1	1	2	0		Neocomian-Aptian	1	-145	-113		Post and Bell, 1961
123	47.0804	-109.189	1	3	0	mod	Aptian-mid Albian	3	-125	-105		Vuke, 2000
124	NA	NA	2	6	0	low	Aptian-mid Albian	3	-125	-105		Vuke, 2000
125	47.43	-111.35	2	5	0	mod	Aptian-mid Albian	3	-125	-105		Vuke, 2000
126	46.9323	-109.555	1	1	0	high	Aptian-mid Albian	3	-125	-105		Vuke, 2000
127	NA	NA	1	2	0	low	Aptian-mid Albian	3	-125	-105		Vuke, 2000
128	47.0667	-109.317	1	2	0	low	Aptian-mid Albian	3	-125	-105		Vuke, 2000
129	47.43	-111.35	3	9	0	mod	Aptian-mid Albian	3	-125	-105		Vuke, 2000
130	47.5224	-111.282	3	15	0	low	Aptian-mid Albian	3	-125	-105		Vuke, 2000
131	47.1	-110.25	1	3	0	mod	Aptian-mid Albian	3	-125	-105		Vuke, 2000
132	47.5	-111.2	1	2	0	mod	Aptian-mid Albian	3	-125	-105		Vuke, 2000
133	46	-113	2	8	0	mod	Aptian-mid Albian	3	-125	-105		Vuke, 2000
134	47.3527	-110.899	1	5	0	mod	Aptian-mid Albian	3	-125	-105		Vuke, 2000
135	47.5333	-111.2	2	10	0	low	Aptian-mid Albian	3	-125	-105		Vuke, 2000
136	32.25	-97.81	3	14	0	low	Albian	3	-119	-106	Fontaine 1893	Mancini and Scott 2006
137	NA	NA	1	2	2	low	Albian	4	-106	-101		Hochuli et al. 2006
138	39.531	-75.973	2	2	2	mod	Albian	4	-106	-101		Hochuli et al. 2006
139	NA	NA	3	2	0	low	Albian	4	-106	-101		Hochuli et al. 2006
140	30.532	-103.22	2	9	0	low	pre-Aptian	1	-145	-119		Hochuli et al. 2006
141	38.9167	-76.9167	3	4	2	low	mid-late Albian	4	-106	-100.5		Hochuli et al. 2006
142	39.528	-75.98	2	5	2	low	late Albian	4	-106	-101		Hochuli et al. 2006
143	39.13	-76.43	2	2	2	low	mid-late Albian	4	-106	-101		Hochuli et al. 2006
144	38.553	-77.23	3	7	2	high	late Albian	4	-104	-101		Hochuli et al. 2006
145	38.41	-77.36	1	2	1	mod	mid-late Albian	4	-106	-101		Hochuli et al. 2006

146	38.41	-77.36	2	3	2	mod	mid-late Albian	4	-106	-101		Hochuli et al. 2006
147	38.41	-77.36	3	5	2	mod	mid-late Albian	4	-106	-101		Hochuli et al. 2006
148	38.41	-77.36	3	5	2	mod	mid-late Albian	4	-106	-101		Hochuli et al. 2006
149	38.39	-77.43	2	9	1	high	early-mid Albian	3	-113	-104		Hochuli et al. 2006
150	37.4237	-77.4247	1	5	1	low	Aptian	3	-119	-110		Hochuli et al. 2006
151	38.84	-77.08	2	11	1	low	Aptian	2	-119	-113		Hochuli et al. 2006
152	37.375	-79.359	3	14	0	low	Aptian	2	-119	-113	Hickey et al. 2010	Hochuli et al. 2006
153	37.375	-79.359	3	19	1	low	Aptian	2	-119	-113	Hickey et al. 2010	Hochuli et al. 2006
154	37.375	-79.359	3	18	1	low	Aptian	2	-119	-113	Hickey et al. 2010	Hochuli et al. 2006
155	37.375	-79.359	1	NA	0	low	Aptian	2	-119	-113	Fontaine 1889	Hochuli et al. 2006
156	37.375	-79.359	1	NA	0	low	Aptian	2	-119	-113	Fontaine 1889	Hochuli et al. 2006
157	37.407	-77.304	1	NA	1	low	mid-late Albian	4	-106	-101	Fontaine 1889	Hochuli et al. 2006
158	37.407	-77.304	1	NA	1	low	mid-late Albian	4	-106	-101	Fontaine 1889	Hochuli et al. 2006
159	37.407	-77.304	1	NA	2	low	mid-late Albian	4	-106	-101	Fontaine 1889	Hochuli et al. 2006
160	37.366	-79.36	1	NA	0	low	Aptian	2	-119	-113	Fontaine 1889	Hochuli et al. 2006
161	37.366	-79.36	1	NA	1	low	Aptian	2	-119	-113	Fontaine 1889	Hochuli et al. 2006
162	38.2983	-77.4545	1	NA	0	low	Aptian-Albian	3	-119	-109	Fontaine 1889	Hochuli et al. 2006
163	38.38	-77.45	1	NA	1	low	Aptian	2	-119	-113	Fontaine 1889	Hochuli et al. 2006
164	38.41	-77.36	1	4	2	low	mid-late Albian	4	-106	-101	Fontaine 1889	Hochuli et al. 2006
165	38.41	-77.36	1	7	2	low	mid-late Albian	4	-106	-101	Ward 1905, p.481	Hochuli et al. 2006
166	38.41	-77.36	3	8	1	mod	mid-late Albian	4	-106	-101	Fontaine 1889	Hochuli et al. 2006
167	38.667	-77.24	1	1	0	low	Aptian	2	-119	-113	Fontaine 1889	Hochuli et al. 2006
168	38.67	-77.23	2	8	1	low	Aptian	2	-119	-113	Fontaine 1889; Ward 1905	Hochuli et al. 2006
169	39.28	-76.608	1	NA	1	low	Aptian-Albian	3	-119	-110	Fontaine 1889	Hochuli et al. 2006
170	38.29	-77.48	1	3	0	mod	Aptian	2	-119	-113	Ward 1905, p.480	Hochuli et al. 2006

171	38.57	-77.262	1	NA	0	low	Aptian	2	-119	-113	Ward 1905	Hochuli et al. 2006
172	38.687	-77.122	1	NA	1		mid-late Albian	4	-106	-101	Ward 1905	Hochuli et al. 2006
173	38.687	-77.122	1	NA	1		mid-late Albian	4	-106	-101	Ward 1905	Hochuli et al. 2006
174	38.687	-77.122	1	NA	1		mid-late Albian	4	-106	-101	Ward 1905	Hochuli et al. 2006
175	38.687	-77.122	1	NA	1		mid-late Albian	4	-106	-101	Ward 1905	Hochuli et al. 2006
176	38.687	-77.122	1	NA	1		mid-late Albian	4	-106	-101	Ward 1905	Hochuli et al. 2006
177	38.687	-77.122	1	NA	1		mid-late Albian	4	-106	-101	Ward 1905	Hochuli et al. 2006
178	38.705	-77.088	1	NA	1		mid-late Albian	4	-106	-101	Ward 1905	Hochuli et al. 2006
179	38.705	-77.088	1	NA	1		mid-late Albian	4	-106	-101	Ward 1905	Hochuli et al. 2006
180	38.705	-77.088	1	NA	1		mid-late Albian	4	-106	-101	Ward 1905	Hochuli et al. 2006
181	38.705	-77.088	1	NA	1		mid-late Albian	4	-106	-101	Ward 1905	Hochuli et al. 2006
182	38.705	-77.088	1	NA	1		mid-late Albian	4	-106	-101	Ward 1905	Hochuli et al. 2006
183	38.705	-77.088	1	NA	1		mid-late Albian	4	-106	-101	Ward 1905	Hochuli et al. 2006
184	NA	NA	2	16	1	low	mid-late Albian	4	-106	-101	Ward 1905	Hochuli et al. 2006
185	NA	NA	1	3	0		mid-late Albian	4	-106	-101	Ward 1905	Hochuli et al. 2006
186	NA	NA	3	20	1	low	upper zone I	3	-119	-109	Ward 1905	Hochuli et al. 2006
187	NA	NA	1	7	1	low	upper zone I	3	-119	-109	Ward 1905	Hochuli et al. 2006
188	NA	NA	1	4	0		upper zone I	3	-119	-109	Ward 1905	Hochuli et al. 2006
189	NA	NA	2	9	0		Aptian	2	-119	-113	Ward 1905	Hochuli et al. 2006
190	NA	NA	1	5	0		upper zone I	3	-119	-109	Ward 1905	Hochuli et al. 2006
191	NA	NA	3	14	1		upper zone I	3	-119	-109	Ward 1905	Hochuli et al. 2006
192	38.772	-77.03	3	25	2		mid-late Albian	4	-106	-101	Ward 1905	Hochuli et al. 2006
193	NA	NA	3	19	1		upper zone I	3	-119	-109	Ward 1905	Hochuli et al. 2006
194	NA	NA	1	5	0		upper zone I	3	-119	-109	Ward 1905	Hochuli et al. 2006
195	NA	NA	1	4	0		Aptian	2	-119	-113	Ward 1905	Hochuli et al. 2006
196	NA	NA	1	2	0		upper zone 1	3	-119	-109	Ward 1905	Hochuli et al. 2006

197	NA	NA	3	16	1		upper zone 1	3	-119	-109	Ward 1905	Hochuli et al. 2006
198	39.279	-77.608	1	NA	1	low	upper zone 1	3	-119	-109	Ward 1905	Hochuli et al. 2006
199	39.279	-77.608	1	NA	1	low	upper zone 1	3	-119	-109	Ward 1905	Hochuli et al. 2006
200	39.279	-77.608	1	NA	1	low	upper zone 1	3	-119	-109	Ward 1905	Hochuli et al. 2006
201	39.279	-77.608	1	NA	1	low	upper zone 1	3	-119	-109	Ward 1905	Hochuli et al. 2006
202	39.279	-77.608	1	NA	1	low	upper zone 1	3	-119	-109	Ward 1905	Hochuli et al. 2006
203	39.279	-77.608	1	NA	1	low	upper zone 1	3	-119	-109	Ward 1905	Hochuli et al. 2006
204	39.279	-77.608	1	NA	1	low	upper zone 1	3	-119	-109	Ward 1905	Hochuli et al. 2006
205	39.279	-77.608	1	NA	1	low	upper zone 1	3	-119	-109	Ward 1905	Hochuli et al. 2006
206	39.48	-75.99	3	28	2	low	zone IIC	4	-101	-95	Wolfe and Upchurch 1987	Hochuli et al. 2006
207	44.38	-123.49	1	NA	0		Berriasian	1	-145	-140	Fontaine in Ward 1905 p. 47	Imlay 1959; Surpless et al. 2006
208	44.38	-123.49	2	NA	0		Berriasian	1	-145	-140	Fontaine in Ward 1905 p. 47	Imlay 1959; Surpless et al. 2006
209	44.38	-123.49	1	NA	0		Berriasian	1	-145	-140	Fontaine in Ward 1905 p. 47	Imlay 1959; Surpless et al. 2006
210	44.38	-123.49	2	6	0		Berriasian	1	-145	-140	Fontaine in Ward 1905 p. 47	Imlay 1959; Surpless et al. 2006
211	44.38	-123.49	1	NA	0		Berriasian	1	-145	-140	Fontaine in Ward 1905 p. 47	Imlay 1959; Surpless et al. 2006
212	44.38	-123.49	1	NA	0		Berriasian	1	-145	-140	Fontaine in Ward 1905 p. 47	Imlay 1959; Surpless et al. 2006
213	44.38	-123.49	3	16	0	mod	Berriasian	1	-145	-140	Fontaine in Ward 1905 p. 47	Imlay 1959; Surpless et al. 2006
214	44.38	-123.49	1	NA	0		Berriasian	1	-145	-140	Fontaine in Ward 1905 p. 47	Imlay 1959; Surpless et al. 2006
215	44.38	-123.49	1	NA	0		Berriasian	1	-145	-140	Fontaine in Ward 1905 p. 47	Imlay 1959; Surpless et al. 2006
216	44.38	-123.49	1	NA	0		Berriasian	1	-145	-140	Fontaine in Ward 1905 p. 47	Imlay 1959; Surpless et al. 2006
217	44.38	-123.49	1	NA	0		Berriasian	1	-145	-140	Fontaine in Ward 1905 p. 47	Imlay 1959; Surpless et al. 2006
218	44.38	-123.49	1	NA	0		Berriasian	1	-145	-140	Fontaine in Ward 1905 p. 47	Imlay 1959; Surpless et al. 2006
219	44.38	-123.49	1	NA	0		Berriasian	1	-145	-140	Fontaine in Ward 1905 p. 47	Imlay 1959; Surpless et al. 2006
220	44.38	-123.49	1	NA	0		Berriasian	1	-145	-140	Fontaine in Ward 1905 p. 47	Imlay 1959; Surpless et al. 2006
221	44.38	-123.49	1	NA	0		Berriasian	1	-145	-140	Fontaine in Ward 1905 p. 47	Imlay 1959; Surpless et al. 2006
222	44.38	-123.49	1	NA	0		Berriasian	1	-145	-140	Fontaine in Ward 1905 p. 47	Imlay 1959; Surpless et al. 2006

223	44.38	-123.49	3	10	0	mod	Berriasian	1	-145	-140	Fontaine in Ward 1905 p. 47	Imlay 1959; Surpless et al. 2006
224	44.38	-123.49	3	9	0	mod	Berriasian	1	-145	-140	Fontaine in Ward 1905 p. 47	Imlay 1959; Surpless et al. 2006
225	44.38	-123.49	3	18	0	low	Berriasian	1	-145	-140	Fontaine in Ward 1905 p. 47	Imlay 1959; Surpless et al. 2006
226	44.38	-123.49	1	NA	0		Berriasian	1	-145	-140	Fontaine in Ward 1905 p. 47	Imlay 1959; Surpless et al. 2006
227	44.38	-123.49	1	NA	0		Berriasian	1	-145	-140	Fontaine in Ward 1905 p. 47	Imlay 1959; Surpless et al. 2006
228	44.38	-123.49	1	NA	0		Berriasian	1	-145	-140	Fontaine in Ward 1905 p. 47	Imlay 1959; Surpless et al. 2006
229	44.0364	-107.516	1	4	0	low	Neocomian	1	-140	-125	Knowlton 1916	Hu, pers. com.
230	44.0346	-107.514	1	4	0	low	Neocomian	1	-145	-125		Hu, pers. com.
231	44.032	-107.51	2	3	1	low	mid-late Albian	4	-104	-101		D'Emic and Britt, 2008
232	44.0327	-107.516	2	12	1	low	mid-late Albian	4	-104	-101		D'Emic and Britt, 2008
233	44.0805	-107.536	2	4	0	low	Neocomian	1	-145	-125		Hu, pers. com.
234			2	6	1	low	mid-late Albian	4	-104	-101		D'Emic and Britt, 2008
235	44.5122	-107.897	2	17	1	low	mid-late Albian	4	-104	-101		D'Emic and Britt, 2008
236	44.5056	-107.855	1	5	1	low	mid-late Albian	4	-104	-101		D'Emic and Britt, 2008
237	44.9845	-108.33	3	7	1	low	early Alban	3	-111	-104		D'Emic and Britt, 2008
238	44.9677	-108.308	2	8	2	high	mid-late Albian	4	-104	-101		D'Emic and Britt, 2008
239	44.967	-108.306	1	3	2	high	mid-late Albian	4	-104	-101		D'Emic and Britt, 2008
240	44.0807	-107.536	2	11	0	low	Neocomian	1	-145	-125		Hu, pers. com.
241	44.9673	-108.307	1	2	1	low	mid-late Albian	4	-104	-101		D'Emic and Britt, 2008
242	44.967	-108.306	2	12	1	low	mid-late Albian	4	-104	-101		D'Emic and Britt, 2008
243	44.967	-108.306	1	4	2	low	mid-late Albian	4	-104	-101		D'Emic and Britt, 2008
244			1	3	1	low	mid-late Albian	4	-104	-101		D'Emic and Britt, 2008

245			1	5	2	mod	mid-late Albian	4	-104	-101		D'Emic and Britt, 2008
246	44.0412	-107.508	1	1	0	low	Neocomian	1	-145	-125		Hu, pers. com.
247	44.9683	-108.309	1	4	2	mod	mid-late Albian	4	-104	-101		D'Emic and Britt, 2008
248	39.652	-105.19	1	1	2	mod	Cenomanian	4	-101	-95	Berry 1933	
249	44.65	-104.217	1	4	1	mod	mid Albian	3	-109	-105		Post and Bell, 1961
250	44.65	-104.217	1	4	1	mod	mid Albian	3	-109	-105		Post and Bell, 1961
251	44.5241	-108.015	2	6	1	low	mid-late Albian	4	-104	-101		D'Emic and Britt, 2008
252	44.9676	-108.308	2	10	2	high	mid-late Albian	4	-104	-101		D'Emic and Britt, 2008
253	44.506	-107.857	2	6	1	low	mid-late Albian	4	-104	-101		D'Emic and Britt, 2008
254	44.523	-108.016	2	13	1	mod	mid-late Albian	4	-104	-101		D'Emic and Britt, 2008
255	39.48	-75.99	2	4	2	low	early Cenomanian	4	-101	-95		Hochuli et al. 2006
256	39.131	-76.431	2	1	0	low		4	-101	-95	Upchurch and Doyle 1981	Hochuli et al. 2006
257	44.0334	-107.516	3	15	0	low	Neocomian	1	-145	-125		Hu, pers. com.
258	44.5098	-107.862	3	20	2	low	mid-late Albian	4	-104	-101		D'Emic and Britt, 2008
259	39.48	-75.99	3	18	2	low	early Cenomanian	4	-101	-95		Hochuli et al. 2006

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